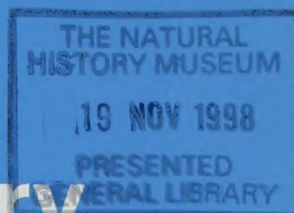


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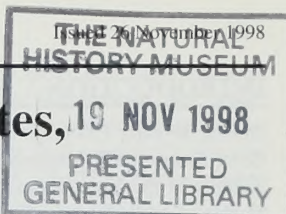
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Caradoc brachiopods from the Shan States, Burma (Myanmar)

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SYNOPSIS. The brachiopod fauna from the Naungkangyi Group and its equivalents in the Shan States, Burma (Myanmar) is described and reviewed, partly from new collections and also from the publications of Reed in the early half of this century. It consists of 37 taxa within 31 genera, of which *Dirafinesquina* (Family Rafinesquinidae) is a new genus, and *Dirafinesquina globosa* and *Leptellina* (*Leptellina*) *minor* are new species. The fauna is of Late Ordovician (Caradoc) age. Affinity analysis between this fauna and other contemporary faunas from South China, North China, Kazakhstan, Altai, Wales, New South Wales and British Columbia shows that the Burmese fauna is most comparable with that from South China, and to a lesser extent North China, and very different from New South Wales and British Columbia. This indicates that the Shan–Thai (Sibumasu) palaeoplate, upon which the Shan States were situated during the Ordovician, was close to the South China palaeoplate.

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INTRODUCTION

During the early 1970s the then Institute of Geological Sciences of Great Britain (IGS) undertook field work on behalf of the United Nations in the Shan States, Burma (a country often now termed Myanmar) with the prime aim of establishing the nature and economic prospects of lead-zinc-silver mineralisation of the area. The rocks studied were Cambrian to Cretaceous in age, with substantial igneous intrusions, and included the Ordovician Naungkangyi Group and its equivalent rocks from which came the brachiopods described here. These were collected by the IGS survey teams, in particular A. H. G. Mitchell and B. J. Amos, and sent to the Natural History Museum, London, for identification amongst other faunas. The results, including the preliminary identifications of the brachiopods by one of us (LRMC) were published in two memoirs and accompanying geological maps: Garson, Amos & Mitchell (1976) for parts of the Southern Shan States (AM and BA in Fig. 1) and Mitchell *et al.* (1977) for parts of the Northern Shan States (AM, TM and YA in Fig. 1). The Naungkangyi Group faunas had also been collected in the early years of the century by the Indian Geological Survey, summarised by La Touche (1913), and the brachiopods published in four papers by Reed (1906, 1915, 1932 and 1936); however, Reed described them somewhat in isolation from contemporary faunas in adjacent parts of Asia. The purpose of the present paper is to reidentify and partially redescribe the Naungkangyi brachiopods in the light of modern brachiopod studies, and to compare them with nearby areas, in particular South China.

BRACHIOPOD FAUNA OF THE NAUNGKANGYI GROUP AND EQUIVALENTS

There follows a list of the fauna which we recognise from the Naungkangyi Group and its equivalents. Those taxa with an asterisk (*) are recorded and figured by Reed (1906, 1915, 1932 and 1936) but were not recollected by the IGS team, and are included here only on the basis of our interpretation of Reed's figures. Reed's original attributions are given in square brackets.

**Lingulella* sp. [*Lingula* cf. *quadrata*: 1906: 49, pl. 4, fig. 1].

**Palaeoglossa*? sp. [*L.* cf. *attenuata*: 1915: 8, pl. 2, fig. 5].

**Schizotreta* sp. [*Schizotreta* cf. *elliptica*: 1906: 50, pl. 4, figs 2, 2a].

Plaesiomys taungtalensis (Reed, 1936) [*Orthis* (*Dinorthis*) *flabellulum*: 1906: 62, pl. 4, figs 4–6].

**Plaesiomys* sp. [*O.* (*Dinorthis*) *porcata birmanica*: 1915: 10, pl. 2, figs 12–13].

**Glyptorthis* sp. [*O.* (*Glyptorthis*) sp.: 1936: 25, pl. 1, fig. 24].

Nicolella sylvatica (Reed, 1936) [*O.* (*Hesperorthis*) cf. *laurentina*: 1936: 20, pl. 1, fig. 15; *O.* (*Wattsella*?) *pontilis*: 1936: 27, pl. 2, figs 5–7].

Nicolella sp. [*O.* (*Nicolella*) cf. *actoniae*: 1936: 29, pl. 2, fig. 9].

**N.* sp. [*O.* (*Plectorthis*) cf. *dichotoma*: 1936: 20, pl. 1, fig. 23].

**N. liberalis* (Reed, 1936) [*O.* (*Eridorthis*) *liberalis*: 1936: 22, pl. 1, figs 3, 3a, 4; *O.* (*E.*) *kalavensis*: 1936: 23, pl. 1, figs 1–2].

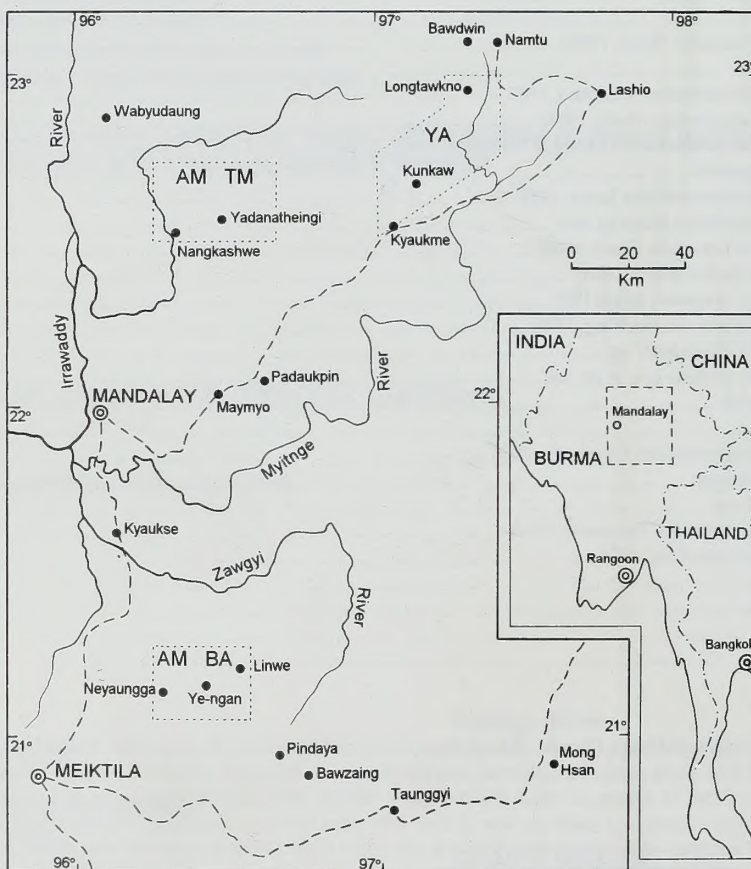


Fig. 1 Location map of Shan States, Burma (Myanmar), with dotted blocks showing the main areas of IGS mapping, which include AM, BA, TM and YA, the prefixes to the new fossil localities and collections described here.

- **Ptychopleurella* sp. [*O. (Ptychopleurella)* cf. *lapworthi*: 1936: 27, pl. 2, fig. 4].
- Saucrorthis irravadica* (Reed, 1906) [*Orthis pustulifera*: 1936: 18, pl. 1, figs 7–14, pl. 2, fig. 3].
- Skenidioides* sp. [*Skenidioides* cf. *billingsi*: 1936: 68, pl. 2, figs 8, 8a].
- **S.* sp. [*O. (Hesperorthis?)* sp.: 1936: 20, pl. 1, fig. 19].
- *Indet. draboviid [*O. (Dalmanella)* *sinchaungensis*: 1936: 28, pl. 2, figs 12–15a].
- **Dalmanella?* sp. [*O. (D.) testudinaria shanensis*: 1915: 9, pl. 2, figs 8, 11].
- Onniella chaungzonensis* (Reed, 1906) [*O. (D.) testudinaria*: 1906: 60, pl. 4, figs 25–26; *O. (D.) testudinaria shanensis*: 1915: 9, pl. 2, figs 6–7, 9–10].
- *Indet. dalmanelloids [*Yeosinella consignata*: 1932: 193, pl. 3, figs 1 1a, 2; 1936: 30, pl. 4, fig. 11].
- Indet. clitambonitid.
- Leptellina (Leptellina) minor* sp. nov. [*Leptelloidea (?Leangella)* cf. *derfelensis*: 1936: 43, pl. 4, figs 24–25; *L. (Leangella)* cf. *shoeshookensis*: 1936: 43, pl. 4, fig. 28].
- *Indet. leptellinids [*Leptelloidea yeosinensis*: 1932: 196, pl. 3, figs 3–6; *L. campestris*: 1936: 42, pl. 3, figs 16–17; *Leptestina?* sp.: 1936: 46, pl. 3, fig. 4].
- **Leangella (Leangella)* sp. [*Plectambonites* cf. *llandeiloensis*, Reed 1915: 13, pl. 3, fig. 3].
- Bekkerella subcrateroides* (Reed, 1906) [*Rafinesquina (Bekkerella) gentilis*: 1936: 38, pl. 4, fig. 14].
- Ishimia subdeltoidea* (Reed, 1906) [*R. (Kjaerina)* cf. *felix*: 1936: 37, pl. 4, fig. 1].
- Ptychoglyptus? shanensis*, Reed, 1932: 195, pl. 3, fig. 15.
- *Indet. sowerbyellids [*Plectambonites repanda*: 1906: 56, pl. 4, fig. 38; *Sowerbyella* cf. *liliifera* var. *triangulum*: 1936: 39, pl. 4, fig. 10].
- *Indet. plectambonitoid [*Plectambonites quinquecostata*: 1906: 55, pl. 4, figs 34–35; *P. sericea*: 1906: 57, pl. 4, figs 36–37].
- Bellimurina (Bellimurina?)* sp.
- *Indet. strophomenids [*Strophomena* sp.: 1915: 12, pl. 3, fig. 1; *Rafinesquina (Kjaerina)* cf. *praecursor*: 1936: 71, pl. 3, fig. 18].
- *Indet. furcitellinid [*R. imbrex*: 1906: 52, pl. 5, figs 9–12].
- Dirafinesquina globosa* gen. et sp. nov. [*R.* cf. *alternata*: 1936: 69, pl. 3, fig. 6; *R.* cf. *semiglobosina*: 1936: 70, pl. 3, fig. 7].
- Indet. leptaenines [*Leptaena* cf. *juvenilis*: 1936: 33, pl. 3, fig. 3; *L.* cf. *richmondensis*: 1936: 34, pl. 3, fig. 11; *L. spectata*: 1936: 34, pl. 3, fig. 12].
- Glyptomena* sp.
- Indet. syntrophopsid.
- Porambonites* spp. [*P. intercedens*: 1906: 68, pl. 5, figs 15, 15a, 15b; *P. sinuatus*: 1915: 14, pl. 3, figs 4–5; *P.* cf. *acutiplicata*: 1936: 48, pl. 3, figs 1–2; *P.* cf. *wahli*: 1936: 49, pl. 3, fig. 15; *Clitambonites* cf. *squamata*: 1906: 66, pl. 5, fig. 14; *C.* cf. *ascendens*: 1936: 31, pl. 3, fig. 14].
- Protozyga? haydeni* Reed, 1936: 51, pl. 4, fig. 12.
- **Cyclospira* sp. Reed, 1936: 52, pl. 4, fig. 13 [*?Hyattidina* sp.: 1932: 206, pl. 3, figs 17, 18].

In addition, Reed figured the following which we find indeterminate, and have therefore omitted both from the above list and also from our faunal analysis of palaeobiogeography (not in this list are other determinations by Reed without any figures):

- Ahtiella?* sp.: 1936: 47, pl. 1, fig. 20; *Clitambonites* cf. *pyron*: 1906: 65, pl. 5, figs 13, 13a; *Chonetes? thebavensis* sp. nov.: 1906: 57, pl. 5, fig. 16 (perhaps an orthoid); *Gonambonites*

(*Antigonambonites*) *emancipatus*: 1936: 67, pl. 1, fig. 25; *Ingria?* sp.: 1936: 47, pl. 4, fig. 2; *Leptaena? ledetensis* sp. nov.: 1906: 54, pl. 4, figs 39–41 (perhaps a plectambonitoid); *Leptelloidea* cf. *leptelloides*: 1936: 73, pl. 4, fig. 9; *L. (Leangella?) lamellata* sp. nov.: 1936: 44, pl. 4, figs 22, 23, 23a (indeterminable plectambonitoid); *Leptestia* cf. *musculosa*: 1936: 45, pl. 3, fig. 8; *Orthis calligramma* var.: 1906: 59, pl. 4, fig. 3; 1915: 11, pl. 2, figs 14, 14a; *O. (Dalmanella) elegantula*: 1906: 60, pl. 4, figs 23–24; *O. (Hesperorthis)* cf. *tricenaria*: 1936: 68, pl. 1, fig. 22; *O. (Platystrophia) bifurcata* var.?: 1915: 10, pl. 2, fig. 15; *O. (Ptychopleurella) pinea* sp. nov.: 1936: 26, pl. 1, figs 18, 18a (indeterminable orthoid); *Petraria* cf. *rugosa*: 1932: 98, pl. 3, fig. 16; *Protozyga?* cf. *obsoleta*: 1936: 52, pl. 5, figs. 9–10; *Rafinesquina* cf. *jaervenensis*: 1936: 71, pl. 3, figs 13, 13a; *R.* (or *Leptaena*) cf. *nubigena*: 1936: 72, pl. 1, fig. 16; *R.* cf. *richardsoni*: 1936: 37, pl. 3, fig. 9; *Skenidioides* cf. *billingsi*: 1936: 68, pl. 2, figs 8, 8a, 16–17; *S.* cf. *oelandicus*: 1936: 30, pl. 2, figs 18–21; *Sowerbyella* cf. *cylindrica*: 1936: 40, pl. 4, fig. 15; *S.* cf. *himalensis*: 1936: 40, pl. 4, fig. 3; *S. wilsoni* sp. nov.: 1936: 41, pl. 4, figs 4–8 (indeterminable plectambonitoid); *Stropheodonta* aff. *corrugatella*: 1915: 12, pl. 3, figs 2, 2a; *Strophomena* cf. *subtenta*: 1936: 35, pl. 3, fig. 10; *S. (Actinomena)* cf. *subarachnoidea*: 1936: 36, pl. 3, fig. 5; *Syntrophina* cf. *affinis*: 1936: 49, pl. 1, fig. 17; *Vellamo nemoralis*: 1936: 31, pl. 1, figs 5–6; *V.* cf. *?simplex*: 1936: 32, pl. 1, fig. 21.

AGE OF THE FAUNA

From the above list, we perceive that the known fauna from the Naungkangyi Group and its equivalents consists of 31 genera, amongst which 32% are orthoids and 42% strophomenoids, and that these two groups are also the most abundant. The absence of rhynchonelloids is an outstanding character of the fauna. Besides the two endemic genera, *Bekkerella* and *Dirafinesquina*, most of the others are limited to the Ordovician, and mostly the Llandeilo to Ashgill. *Plaesiomys* is widely distributed and all its occurrences are of Caradoc and Ashgill age, so is *Nicolella*, which is also found in the early Caradoc Shihtzupu Formation of South China. The *Saucrorthis* in our fauna is its first record outside South China, where it is reported only from the Shihtzupu Formation. *Onniella* is of Caradoc to Ashgill age with its acme in the Caradoc. Most of the known species of *Protozyga* are limited to the early to middle Caradoc of North America, north-west Europe and south-east Asia (Copper 1986: 834). *Cyclospira* ranged from the Caradoc to the Ashgill, and was particularly common in the late Caradoc (Copper 1986: 847). *Ishimia* is known from Llanvirn to early Caradoc rocks, *Ptychoglyptus* from the Caradoc to the Ashgill, *Bellimurina* only from the Caradoc and *Glyptomena* from the Llandeilo to the Caradoc. Once again, *Leptellina (Leptellina)*, *Leangella (Leangella)*, *Bellimurina*, *Leptaena (Leptaena)* and *Glyptomena* are also known in the Shihtzupu Formation of South China. Fortey & Cocks (1998) have also discussed the age of the Upper Naungkangyi Beds. Thus the faunas studied here from the Naungkangyi Group and its equivalents in the Shan States are probably of Caradoc age. At what period within the Caradoc these rocks were deposited is less certain. Any age above the early Caradoc would extend upwards the ranges of *Saucrorthis* and *Ishimia*. However, since the Naungkangyi Group is more than 2000m thick, then a variety of ages may be represented.

However, in addition to the faunas discussed above, there are clearly also some earlier Ordovician brachiopods occurring in the Shan States. Reed (1932: 182, pl. 3, figs 7–14) described and figured

what he identified as the new species *Orthis (Dalmanella) emancipata* from Bawzaing, which he listed together with some unfigured molluscs, crinoids and the trilobite *Ogygites cf. yunnanensis* Reed. Later he listed and described a further fauna from the Namnoi Horizon, Southern Shan States (Reed 1936: 82), including the new brachiopod *Orthis (Paurorthis) hehoensis* together with trilobites such as undoubted *Annamitella* which Dr R. A. Fortey confirms is restricted to beds no younger than Llandeilo, and is more probably of Llanvirn age. Comparably, also from the Southern Shan States, the Natural History Museum possesses several blocks (BC 52144–52153) from Twinzontaung, collected and presented by T. O. Morris in 1929. These contain hundreds of specimens, mostly external moulds of a monospecific although unidentified orthoid which again has an earlier Ordovician aspect.

There is also the latest Ordovician (Hirnantian) fauna from the Panghsa-pyé Beds, originally described by Reed (1915) and revised by Cocks & Fortey (1997). Thus there are at least three Ordovician horizons present in the Shan States, (a) the Llanvirn-Llandeilo, (b) the Caradoc fauna described here, and (c) late Ashgill faunas from the Panghsa-pyé Beds.

FAUNAL ASSOCIATIONS

Much of the new Naungkangyi material comes from localities AM77 and AM78 north-west of Linwe in the Nyaungga-Ye-ngan area, Southern Shan States (Mitchell *et al.* 1977) at longitude 96°33'E and latitude 21°14'N. The material was collected by A.H.G. Mitchell as blocks, which were split up in the Natural History Museum by one of us (LRMC). Collection AM77 yielded 45 specimens, of which 20 (44.4%) were *Saucrorthis irravadica*, 7 (15.6%) were *Leptellina (Leptellina) minor* and one was *Onniella chaungzonensis*; the remainder were 7 varied bryozoans (15.6%), 9 crinoids (20%) and a single conulariid. Collection AM78 yielded 185 specimens of which 122 (65.9%) were *Leptellina (Leptellina) minor*, 23 (12.4%) were *Dirafinesquina globosa* and one each were *Nicolella sylvatica*, *Glyptomena* sp. and another unidentified orthoid, together with 21 (11.4%) crinoids, 5 (2.7%) the trilobite *Neseuretus birmanicus*, 3 (1.6%) various bryozoans, 5 (2.7%) gastropods of three different kinds, and one conulariid. Even though most of the brachiopods were disarticulated and formed part of a shell hash, the fact that 62 ventral valves and 60 dorsal valves of *Leptellina (Leptellina) minor* were counted in AM78 indicates, nevertheless, that the distance of transportation from the original life habitat to the area of final burial is unlikely to have been great.

All the other material at our disposal were either small collections or single isolated museum specimens from a wide variety of localities. Thus a proper assessment of the associations and hence communities of the Naungkangyi Group must await more substantial systematic collecting. However, even with the small amount of material available, it is clear that the brachiopod diversity of the Naungkangyi Group, although quite large when the Group is considered as a whole, is nevertheless rather small when the individual localities and horizons are considered separately. This diversity is much less than, for example, in the neighbouring Shihtzupu Formation in South China, from which individual beds have yielded over 20 different brachiopods from lithologies which are broadly similar to the Naungkangyi Group. The conclusions reached are that the Naungkangyi associations known to us probably colonized only the shallower parts of the contemporary Ordovician shelf and that the contemporary middle to deeper water faunas are either not preserved or have not yet been found.

PALAEOGEOGRAPHICAL ANALYSIS

The Ordovician was a period of continental dispersal (Cocks & Fortey 1990) and southeast Asia has been recognized as consisting of a number of terranes, one of which is the Sibumasu (or Shan-Thai) terrane including much of the Malay Peninsula, West Thailand, Burma and western Indonesia. The Indochina terrane lies immediately to the east of Sibumasu and the South China terrane to the northeast (Mitchell 1981, Burrett *et al.* 1990). The tectonic boundaries of the Sibumasu terrane are the Uttaradit-Nan to Raub-Bentong sutures to the east and the Shan boundary to the west (Bender 1983, Metcalfe 1992). The Shan States of Central to North Burma (Fig. 1) lie in the western part of the Sino-Burman Ranges. The Naungkangyi Group and its equivalents in the Shan States were deposited at the northern end of the Sibumasu palaeocontinent in the Late Ordovician. From the marine benthic shelly fossils found in these rocks, we can evaluate its relationships with other contemporary terranes. Table 1 shows the faunal affinity indices between eight Caradoc brachiopod faunas calculated by three different formulae as recommended by Rong *et al.* (1995) (for faunal lists see Appendix).

1. The Caradoc Naungkangyi fauna is closest to the early Caradoc Shihtzupu Formation fauna of South China (Xu *et al.* 1974). During the later Caradoc, the purple-red Pagoda Limestone was deposited on the vast area of the Yangtze Platform with a deep-water *Foliomena* fauna quite different from the shallower-water (probably BA2 to BA3 according to Boucot's (1975) concept of Benthic Assemblages) Naungkangyi fauna. There are many common components between the Naungkangyi and Shihtzupu faunas: some genera (such as *Saucrorthis*) are only recorded from these two areas. This confirms that the South China and Sibumasu terranes were not far apart, a relationship which continued into the Ashgill (Cocks & Fortey 1997, Fortey & Cocks 1998).
2. The Naungkangyi fauna shares some similarity with the Caradoc fauna of the Bala District, Wales (Williams 1963), as is shown by the nine common genera, *Lingulella*, *Nicolella*, *Skenidioides*, *Dalmanella*, *Onniella*, *Sowerbyella*, *Glyptomena*, *Bellimurina* and *Cyclospira*. However, these nine genera are widespread or even cosmopolitan, and thus the data indicate only that the Naungkangyi fauna was faunally connected to many other areas in Caradoc times.
3. Also similar to the Naungkangyi fauna is the one from the late Caradoc Pingliang Formation of Shaanxi, North China (Fu 1982, Rong & Zhan 1996). This fauna overlies graptolitic shales and underlies the even shallower-water Beiguoshan Formation fauna of Ashgill age (Rong & Zhan 1996), and thus represents the transition between shallow and deep water faunas. The constituents in common with the Naungkangyi fauna are *Skenidioides*, *Leangella* (*Leangella*), *Sowerbyella* and *Bellimurina*, but in addition there are some typical representatives of the deeper-water *Foliomena* fauna, including *Foliomena* itself. Since the Pingliang fauna has a comparatively high affinity index with the Shihtzupu fauna of South China, we can postulate that South China, North China and Sibumasu were close together during the Late Ordovician, with North China a little further away from the other two, and that the faunas on them were controlled by comparable environmental factors.
4. The Caradoc fauna from New South Wales, Australia (Percival 1991) has no common constituents with any of our listed contemporary faunas apart from cosmopolitan genera such as *Ptychopleurella*, *Skenidioides* and *Sowerbyella*. This is also true of the mid Ashgill (Zhan & Cocks 1998), and indicates that Australia

Table 1 Affinity indices between eight Caradoc brachiopod faunas. BUR, the present fauna; SCH, Guizhou, South China; NCH, Shaanxi, North China; KAZ, Chingiz, Kazakhstan; ALT, Gorny Altai, Russia; WAL, Bala, Wales; NSW, New South Wales, Australia; BCC, British Columbia, Canada (for stratigraphy and references see text). Three numbers are shown for each relationship following the different formulae discussed by Rong *et al.* (1995) in the lower left part of the diagram and their averages in the upper diagonal.

	BUR	SCH	NCH	KAZ	ALT	WAL	NSW	BCC
BUR	1	0.3373	0.2557	0.1063	0.1135	0.2752	0.0388	0.0480
SCH	0.3708 0.3600 0.2810	1	0.1842	0.0222	0	0.1726	0.0580	0.0165
NCH	0.2884 0.2800 0.1986	0.2226 0.2222 0.1079	1	0.0800	0.1039	0.3156	0.0997	0.1138
KAZ	0.1391 0.1304 0.0493	0.0626 0.0625 -0.0586	0.1185 0.1176 0.0038	1	0.0178	0.0567	0.0169	0
ALT	0.1437 0.1429 0.0539	0	0.1376 0.1364 0.0376	0.0516 0.0500 -0.0484	1	0.1064	0.1218	0.1410
WAL	0.3036 0.3030 0.2191	0.2050 0.1923 0.1205	0.3490 0.3333 0.2645	0.0873 0.0800 0.0028	0.1352 0.1333 0.0507	1	0.0691	0.0448
NSW	0.0691 0.0678 -0.0207	0.0907 0.0889 -0.0055	0.1325 0.1304 0.0362	0.0497 0.0476 -0.0465	0.1540 0.1538 0.0577	0.0976 0.0968 0.0131	1	0.0517
BCC	0.0784 0.0769 -0.0114	0.0529 0.0526 -0.0562	0.1502 0.1500 0.0411	0	0.1746 0.1739 0.0746	0.0738 0.0714 -0.0107	0.0840 0.0833 -0.0122	1

was in poor faunal contact with South China and Sibumasu in the Late Ordovician, even though they were both parts of Gondwana. The Caradoc faunas from Kazakhstan and Altai are greatly different from the Naungkangyi fauna; a result which is in contrast with the findings of Zhan & Cocks (1998), which indicated that those two terranes were closely related faunally to the South China terrane in mid Ashgill time.

5. The comparatively deeper-water *Bimuria* fauna of North America described by Jin & Norford (1996) from the Advance Formation in the northern Rocky Mountains, British Columbia, has extremely low similarities with any other contemporary faunas compared here, which indicates that all the other seven sites were far away from Laurentia in Caradoc times.

Thus this brachiopod faunal analysis supports Fortey & Cocks' (1998) conclusions that during the Late Ordovician the Sibumasu terrane was closely related to South and North China, and that Sibumasu was closer to South China, in contrast with the latter's closeness to North China in the Early Ordovician.

SYSTEMATIC PALAEONTOLOGY

The figured and cited specimens are deposited in the Natural History Museum, London (BB and BC) and the Sedgwick Museum, Cambridge (SMA). Dimensions (in mm) are L = length, W = width, L_1 =

length of cardinalia or ventral muscle field, L_2 = distance of the anterior end of dorsal muscle field away from the umbo, W_1 = width of cardinalia or ventral muscle field, W_2 = width of dorsal muscle field, N = number of ribs, α = angle between the socket ridges or brachiophores.

Superfamily **LINGULOIDEA** Menke, 1828

Family **LINGULIDAE** Menke, 1828

Genus **PALAEOGLOSSA** Cockerell, 1911

Palaeoglossa? sp.

1915 *Lingula* cf. *attenuata* Sowerby; Reed: 8, pl. 2, fig. 5.

DISCUSSION. *Lingula* cf. *attenuata* was described by Reed (1915) from the Upper Naungkangyi Group (late Caradoc) of Man-ngai, Northern Shan States, and is tentatively attributed to the genus *Palaeoglossa* here, since Sowerby's *attenuata* is now the type species of that genus (Cocks 1978). However, no original material from the Burmese Ordovician is available to us and we are hesitant to identify the species. In addition, Reed (1906: 49, pl. 4, fig. 1) also listed *Lingula* cf. *quadrata* Eichwald from the Naungkangyi Group of Palin, Northern Shan States. This latter might be reassigned to the oboloid *Lingulella* using the differences between *Lingula* and *Lingulella* featured in Williams *et al.* (1965) and Holmer (1989).

Superfamily **ORTHOIDEA** Woodward, 1852
 Family **PLAESIOMYIDAE** Schuchert, 1913
 Subfamily **PLAESIOMYINAE** Schuchert, 1913
 Genus **PLAESIOMYS** Hall & Clarke, 1892

Plaesiomys taungtalensis (Reed, 1936) Pl. 1, figs 1–5

- 1906 *Orthis* (*Dinorthis*) *flabellulum* Sowerby; Reed: 62, pl. 4, figs 4–6.
 1936 *Orthis* (*Glyptorthis*) *taungtalensis* Reed: 24, pl. 2, figs 10, 10a, 11.

MATERIAL AND LOCALITIES. One dorsal valve (external and internal moulds) from Chaungzon, longitude 96°52'E, latitude 22°21'N; one dorsal external mould from Naungkangale; and two dorsal valves (external and internal moulds) from Pangmaklang (about 20 km northeast of Kunkaw, Locality YA 365, longitude 97°16'E, latitude 22°42'N); all from the Naungkangyi Group of the Northern Shan States.

DISCUSSION. *Plaesiomys* and *Dinorthis* are both large orthoids with relatively small cardinalia and long and elevated sub-triangular to subpentagonal ventral muscle fields (Wright 1964), but the former has multibranching costellae and the latter has simple costae. All the present specimens have branching costellae and small but well-developed cardinalia (about one quarter shell length) with a highly projecting plate-like cardinal process which is limited to the variably-developed notothyrial platform, and so they are included in the genus *Plaesiomys*, although no ventral valves are available.

Reed (1906) described and illustrated three specimens from the Naungkangyi Group at Chaungzon as Sowerby's species *flabellulum* under the subgenus *Dinorthis*, which are the same species as our material in ribbing and dorsal interior. However, the true *flabellulum* (Williams 1963: 363, pl. 3, figs 1–4) has simple costae which only exceptionally branch. *Orthis* (*Glyptorthis*) *taungtalensis* (Reed 1936) was named from the Naungkangyi Series of Taungtala, Southern Shan States, and has branching ornamentation, a very convex dorsal valve and small cardinalia limited to the notothyrial platform, which are all present in our material and typical of *Plaesiomys*. *Orthis* (*Dinorthis*) *porcata birmanica* (Reed 1915: 10, pl. 2, figs 12–13) is another species from the Upper Naungkangyi Group at Ta-Pangtawng of the Northern Shan States which should be reassigned to *Plaesiomys*, but it differs from *taungtalensis* (including Reed's specimens of '*flabellulum*') in having a more circular shell, denser costellae and a more elongate and anteriorly bilobed ventral muscle field.

The type species of *Plaesiomys*, *Orthis subquadrata* (Hall 1847: 126, pl. 32A, figs 1a–o) from the Richmondian (late Caradoc and early Ashgill) of Ohio, USA, differs from *taungtalensis* in having much denser costellae and a much stronger and larger crenulated myophore. *Plaesiomys robusta* and *Plaesiomys multiplicata*, both from the late Caradoc of Glyn Ceiriog, Wales (Bancroft 1945), are very similar to *taungtalensis*, but can be distinguished by their more rounded shell, denser costellae, and different shape of ven-

tral muscle field. *Plaesiomys porcata* (M'Coy), from the Portrane Limestone (Caradoc), Ireland (Wright 1964: 187, pl. 4, figs 1–12), is different from *taungtalensis* in having an 'isolated' cardinal process (without any notothyrial platform).

Family **PRODUCTORTHIDAE** Schuchert & Cooper, 1931
 Subfamily **PRODUCTORTHINAE** Schuchert & Cooper, 1931

Genus **NICOLELLA** Reed, 1917

Nicolella sylvatica (Reed, 1936) Pl. 1, figs 6–10

- 1936 *Orthis* (*Glossorthis*) *sylvatica* Reed: 21, pl. 2, figs 1–2.
 ?1936 *Orthis* (*Hesperorthis*) cf. *laurentina* Billings; Reed: 20, pl. 1, fig. 15.
 ?1936 *Orthis* (*Wattsella*?) *pontilis* Reed: 27, pl. 2, figs 5–7.

MATERIAL AND LOCALITY. Four ventral external, six internal, and two dorsal valves (internal and external moulds) from the Li-lu Formation (upper part of Naungkangyi Group) at Ta-Pangtawng (about 10 km east of Longtawno, Locality YA454.1, longitude 96°23'E, latitude 22°58'N) in the Northern Shan States.

DESCRIPTION. *Exterior.* Semicircular shell 4.5–9.1 mm long and 6.8–11.5 mm wide with the length/width ratio 0.66–0.79. Lateral profile ventri-biconvex, gently convex dorsal valve with a clear sulcus originating from the umbo. Maximum width along the hinge line which extends laterally, forming a small ear. Curved and small ventral interarea apsacline; narrow dorsal interarea anacline. Anterior commissure slightly sulcate. Ornament of 15–19 simple costae occasionally with some branching in the postero-lateral parts. No median costa on dorsal valve but a pair of comparatively weaker costae appear beside the median groove. Closely-spaced concentric growth lines well-developed on some specimens on the anterior one-third of the shell and showing several typically productorthid imbrications. No exopunctae observed.

Ventral interior. Strong triangular teeth supported by thin, short and subparallel dental plates. Small, elongately oval and weakly-impressed muscle field without any apparent anterior or antero-lateral bounding ridges; the adductor and diductor scars are not distinguishable. Strong ribs on the surface of the shell, reflected on the internal surface of both valves in a series of corresponding deep and narrow radial grooves which include the muscle field; the intervals between grooves are almost three times as wide as the groove. No vascular markings seen.

Dorsal interior. Small cardinalia about one-fifth shell length and width; strong cardinal process with a swollen myophore, separated from the brachiophores, occupying the whole notothyrial platform which is slightly elevated; brachiophores triangular at their bases, projecting highly anteriorly and ventrally at about 75° to one another; weak brachiophore supports extend medially and meet at the median ridge to form a low and wide ridge parallel to the hinge line. Poorly impressed muscle field with a low and wide myophragm extending to the anterior margin.

PLATE 1

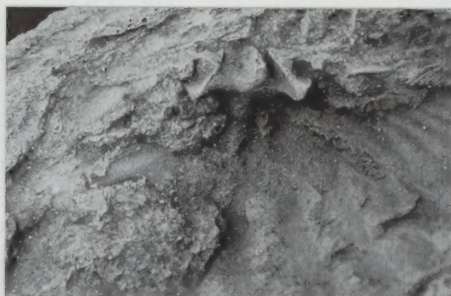
Figs 1–5 *Plaesiomys taungtalensis* (Reed). 1, BC 52159, Kunkaw, Locality YA43, dorsal internal mould, $\times 2$. 2, BB 37726, Pangmaklang, Locality YA365, latex cast of a dorsal internal mould showing the cardinalia, $\times 4$. 3, SMA 3132, Chaungzon, latex cast of a partial dorsal external mould, $\times 2$. 4a, 4b, SMA 3131, Chaungzon, dorsal internal mould and latex cast, $\times 2$. 5, BB 37724, Pangmaklang, Locality YA365, dorsal internal mould, $\times 2.5$.

Figs 6–10 *Nicolella sylvatica* (Reed). 6–9, Ta-Pangtawng, Locality YA454.1. 6a–c, BB 37738, latex casts of ventral exterior and interior, and ventral internal mould, $\times 3$. 7a, 7b, BB 37736, dorsal internal mould and latex cast, $\times 4$. 8a–c, BB 37739, 8a, latex cast of dorsal exterior with a ventral exterior at the top right (BC 52414), $\times 4$; 8b, 8c, latex cast and internal mould of dorsal interior, $\times 4$. 9a, 9b, BC 52414, latex cast and internal mould of ventral interior, $\times 4$. 10a, 10b, BB37682, Nyaungga, Locality BA490, latex cast and internal mould of ventral interior, $\times 4$.

Fig. 11 *Saucrorthis irravadica* (Reed). BB37705, Linwe, Locality AM77, latex cast and internal mould of ventral interior, $\times 4$.



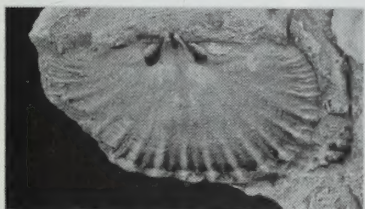
1



2



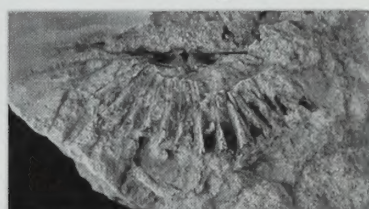
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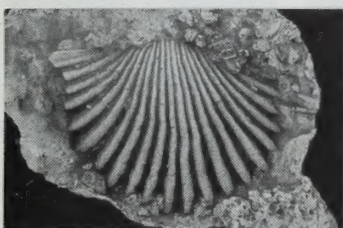
4a



4b



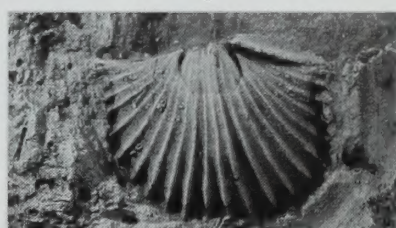
5



6a



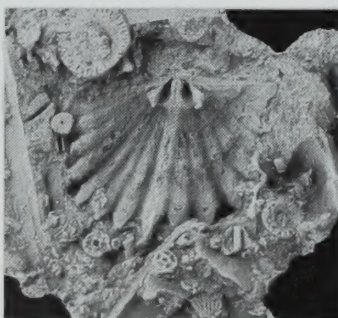
6b



6c



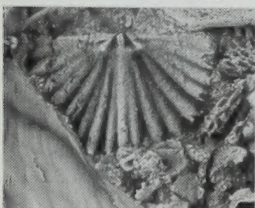
7a



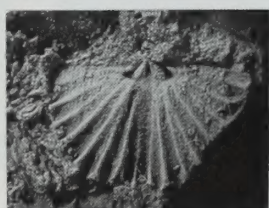
7b



8a



8b



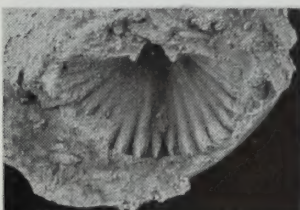
8c



9a



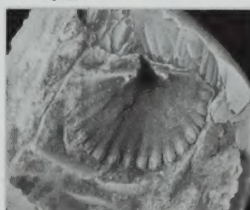
9b



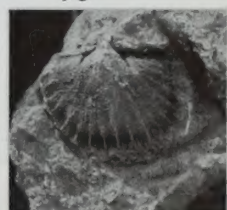
10a



10b



11a



11b

MEASUREMENTS

	L	W	L/W	W1	W1/W	N
BB37736, dorsal valve	6.0	—	—	1.8	—	16
BB37737, ventral valve	5.2	7.0	0.74	2.1	0.30	15
BB37738, ventral valve	9.1	11.5	0.79	3.1	0.27	19
BB37739, dorsal valve	4.5	6.8	0.66	1.3	0.19	16
BB37743, ventral valve	6.2	8.1	0.77	1.9	0.23	15

DISCUSSION. According to Williams' (1963: 352) emended diagnosis, *Nicolella* has a plano-convex shell, an ornament of simple costae with a very few rarely developed costellae, strong teeth supported by short receding dental plates, an elongately oval ventral muscle field without any bounding ridges, and small cardinalia with an elevated notothyrial platform. Both Reed's (1936) illustrated specimen and our present material possess these main characters. The specimen identified by Reed (1936: 20, pl. 1, fig. 15) as *Orthis* (*Hesperorthis*) cf. *laurentina* Billings is a slightly distorted dorsal valve from the rocks corresponding to the Naungkangyi Group in the Southern Shan States of the same age as *sylvatica*. Its outline, ribbing and concentric growth lines are similar to *sylvatica*, but without interiors is only questionably reassigned here to *sylvatica*. Although *Orthis* (*Wattsella*?) *pontilis* (Reed 1936: 27, pl. 2, figs 5–7) has a similar locality and horizon to *sylvatica* and the same exteriors as the latter, its large ventral muscle field and apparent dorsal muscle bounding ridges make us uncertain whether or not it is truly a junior synonym of *sylvatica*.

The type species of *Nicolella*, *Orthis actoniae* J. de C. Sowerby, has been studied and discussed by several authors, such as Davidson (1868: 252, pl. 36, figs 5–17), Williams (1963: 353, pl. 1 figs 15–19, text-fig. 6) and Wright (1964: 165, pl. 2, figs 1–7, 10–11), all from Caradoc material. It differs from *sylvatica* in having more widely divergent brachiophores and in lacking the slight fold and sulcus. *Nicolella delicata* (Xu, Rong & Liu 1974: 151, pl. 66, figs 28–30), from the Shihtzupu Formation (early Caradoc) of Zunyi, Guizhou Province, South China, can be distinguished from *sylvatica* by having well-developed exopunctae and stronger dental plates enclosing a more circular ventral muscle than *sylvatica* and might even be attributable to *Sulevorthis*. *O. (Eridorthis) liberalis* (Reed 1936: 22, pl. 1, figs 3, 3a, 4) and *O. (Eridorthis) kalavensis* (Reed 1936: 23, pl. 1, figs 1–2) are two new species named by Reed on the basis of a ventral and a dorsal valve respectively. Because they are both from the rocks corresponding to the Naungkangyi Group at Taungtala of the Southern Shan States and have similar ribbing and shell sizes, we think they might be the same species and, if so, *liberalis* would be the senior synonym. It differs from *sylvatica* in having much coarser and branching ribs and a sessile pseudospondylium in the ventral interior; however, with the minimal material available, its generic attribution is doubtful.

Nicolella sp.

1936 *Orthis* (*Nicolella*) cf. *actoniae* Sowerby; Reed: 29, pl. 2, fig. 9.

MATERIAL AND LOCALITIES. Two dorsal and one ventral external moulds from the Naungkangyi Group at Kunkaw; four dorsal and two ventral external moulds from the Naungkangyi Group at Chaungzon, both in the Northern Shan States; and one ventral external mould from the rocks corresponding to the Naungkangyi Group at Nyaungga in the Southern Shan States.

DISCUSSION. Reed illustrated only exteriors, which makes further identification unreliable, although the external morphology is similar to *Nicolella actoniae* J. de C. Sowerby from Shropshire. These Burmese specimens differ from *N. sylvatica* in having nearly flat dorsal valves and branching ribs (costellae) at two-thirds of their shell length.

Genus *SAUCRORTHIS* Xu, Rong & Liu, 1974

Saucrorthis irradadica (Reed, 1906) Pl. 1, fig. 11; Pl. 2, figs 1–5

1906 *Orthis irradadica* Reed: 62, pl. 4, figs 15–22.

1915 *Orthis irradadica* Reed; Reed: 11.

?1932 *Yeosinella consignata* Reed: 193, pl. 3, figs 1–2.

?1936 *Orthis pustulifera* Reed: 18, pl. 1, figs 7–14; pl. 2, fig. 3.

1936 *Yeosinella consignata* Reed; Reed: 30, pl. 4, fig. 11.

MATERIAL AND LOCALITIES. One dorsal internal and external, and one ventral external mould from the Naungkangyi Group at Namyun (about 7 km southeast of Longtawko), Northern Shan States; eight ventral internal, nine external, five dorsal internal and eight external moulds at Linwe (Locality AM77), three ventral internal and external, and four dorsal internal and external moulds from the Nyaungga-Ye-ngan area (Locality BA490), both from the Kinle Siltstone Formation (equivalent to the Upper Naungkangyi Group) in the Southern Shan States.

DESCRIPTION. *Exterior*. Small semicircular shell 2.4–6.6 mm long, 3.3–9.1 mm wide, with length/width ratio 0.70–0.88. Lateral profile ventribiconvex with dorsal valve gently convex or even flat with a median sulcus. Maximum width invariably along the hinge line. Ventral interarea comparatively large, apsacline, delthyrium open. Very small anacline dorsal interarea without chilidium, but most of the notothyrium is occupied by the cardinal process. Ornament of simple costae and fine concentric fila. Sharp costae generally unbranching, coarser anteriorly, 18 on the dorsal valve and 15 on the ventral valve irrespective of the shell size; no central costa on dorsal valve. In a well-preserved specimen (Pl. 2, fig. 5), minute but distinct

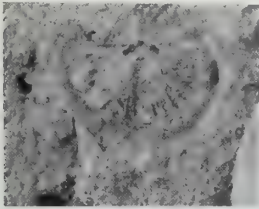
PLATE 2

Figs 1–5 *Saucrorthis irradadica* (Reed). 1a, 1b, BB 37670, Nyaungga, Locality BA490, dorsal internal mould and latex cast, $\times 5$. 2–5, Linwe, Locality AM77; 2, BB 37702, ventral internal mould, $\times 5$; 3, BC 52411, latex cast of dorsal exterior, $\times 4$; 4a–c, BB 37668, 4a, dorsal internal mould, $\times 5$, and 4b, 4c, latex casts of dorsal exterior and interior, $\times 4$; 5, BB 37695, dorsal external mould showing sparse exopunctae, $\times 12$.

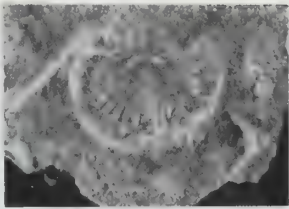
Figs 6–10 *Onniella chaungzonensis* (Reed). 6, BB 37676, Nyaungga, Locality BA490, latex cast of ventral exterior, $\times 4$. 7–10, Ta-Pangtawng, Locality YA454.1. 7a, 7b, BB 37731, latex cast of dorsal exterior, and dorsal internal mould, $\times 4$. 8, BC 52412, ventral internal mould, $\times 8$. 9, BC 52413, latex cast of dorsal exterior with ventral interarea, $\times 8$. 10a, 10b, BC 52416, latex cast and internal mould of dorsal interior with a ventral valve (BC 52415) of *Nicolella sylvatica* (Reed), $\times 4$.

Figs 11–12 Indeterminate clitambonitid. Kunkaw. 11, BB 37777, Locality YA40.1, ventral internal mould, $\times 5$. 12, BB 37771, Locality YA39, ventral internal mould, $\times 3$.

Figs 13–14 *Leptellina* (*Leptellina*) *minor* sp. nov. Linwe, Locality AM78. 13a, 13b, BB 37633, dorsal internal mould, and latex cast, $\times 4$. 14a–c, BB 37643, ventral internal mould, latex cast and posterior view, $\times 5$.



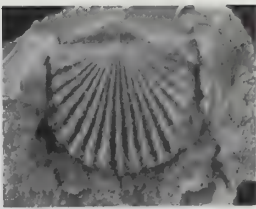
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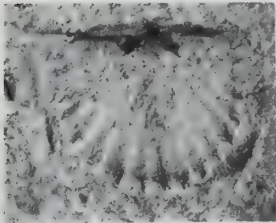
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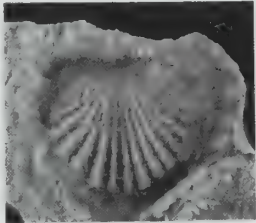
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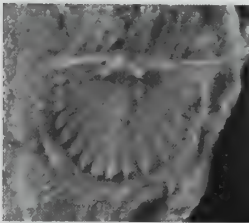
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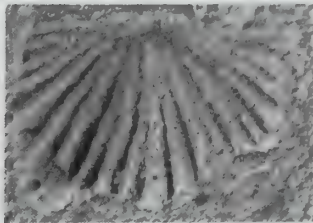
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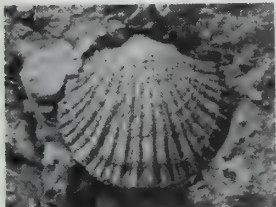
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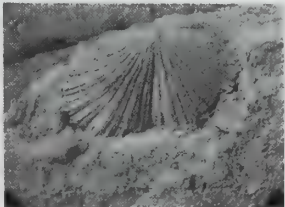
4c



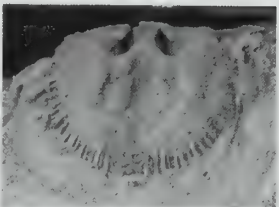
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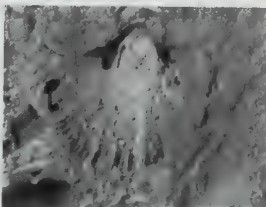
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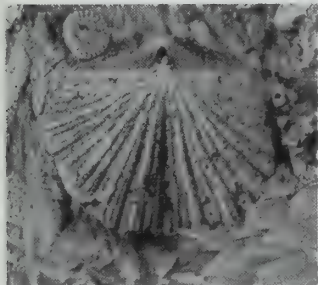
7a



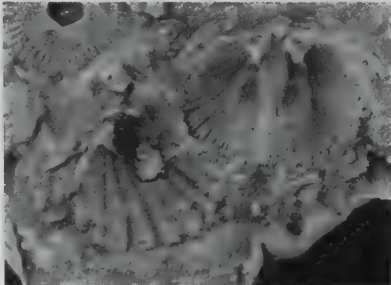
7b



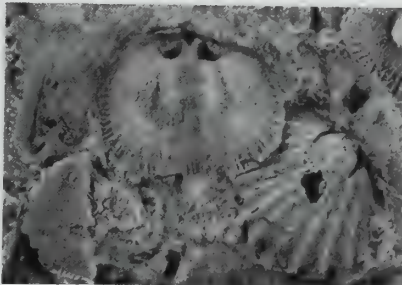
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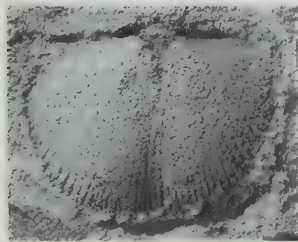
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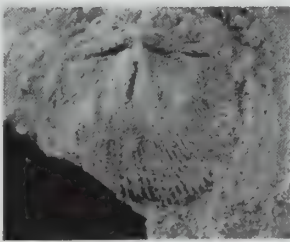
10a



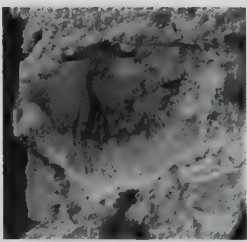
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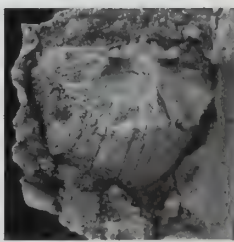
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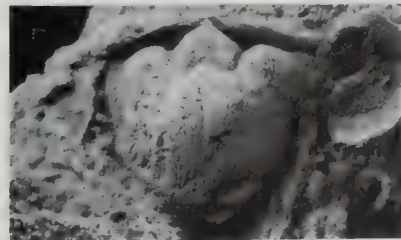
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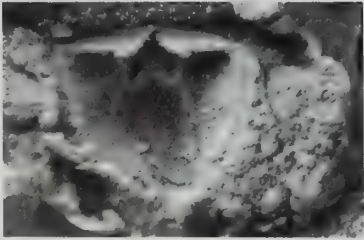
13a



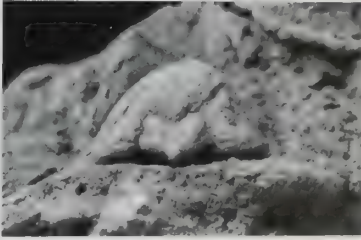
13b



14a



14b



14c

exopunctae are visible in lines along the rib crests, with a few additional exopunctae sporadically distributed on the rib slopes.

Ventral interior. Small teeth supported by a pair of very short, subparallel dental plates. Poorly impressed muscle field about 28% as wide as the shell and open anteriorly. Strong crenulations along the peripheral area of both valves about one quarter of the shell length, which form broad, flat to weakly hollowed, scalloped ridges separated by narrow deep grooves.

Dorsal interior. Cardinalia about one fourth as wide and one sixth as long as the shell; small cardinal process limited to the posterior part of the narrow but weakly elevated notothyrial platform, and connected with the posterior ends of the brachioophores on both sides. Well-developed brachioophores triangular at their base, highly projecting anteriorly and ventrally at 90–110° to one another, and supported for their posterior one-third by thin subparallel plates. Weakly-impressed subquadrate muscle field just in front of the cardinalia, composed of two pairs of adductor scars on either side of a low and wide myophragm which becomes wider anteriorly towards the shell margin; the posterior scars always larger than the anterior pair.

MEASUREMENTS

	L	W	L/W	W ₁	W ₁ /W	N
BB37668, dorsal valve	4.7	5.5	0.85	1.4	0.25	18
BB37669, dorsal valve	3.0	3.7	0.81	0.9	0.24	18
BB37670, dorsal valve	2.4	3.3	0.73	0.9	0.27	18
BB37682, ventral valve	4.5	6.4	0.70	1.8	0.28	15
BB37702, dorsal valve	4.7	5.3	0.88	—	—	18
BB37705, ventral valve	4.2	5.2	0.81	1.5	0.28	15
B29665, dorsal valve	6.6	9.1	0.73	2.6	0.28	—

DISCUSSION. The species *irravadica* was named by Reed (1906) within the genus *Orthis* for some small specimens from the Naungkangyi Group at several localities in the Northern Shan States. The illustrated exteriors and ventral interiors (Reed 1906: pl. 4, figs 15–22) are similar to our specimens from the same area and are assigned to *Saucrorthis* especially on the ribbing and cardinalia. *Orthis pustulifera* Reed (1936: 18, pl. 1, figs 7–14; pl. 2, fig. 3), from rocks corresponding to the Naungkangyi Group at Thittekoon and Konleau, Southern Shan States, is much like *irravadica* in its external characters and cardinalia, but it has better-preserved exopunctae and stronger dorsal muscle bounding ridges and dental plates. The species is questionably included as a junior synonym of *irravadica*. The material identified by Reed (1932, 1936) as *Yeosinella consignata* Reed consists of some dorsal valves from rocks corresponding to the Naungkangyi Group at Ye-o-sin in the Southern Shan States which seem identical to our specimens of *irravadica*. No ventral valves of *consignata* are known, but should they also prove to be the same as *irravadica*, then *Yeosinella* would become a senior synonym of *Saucrorthis*.

Saucrorthis, previously thought endemic to South China, is recorded here from outside it for the first time. The type species, *S. minor* (Xu, Rong & Liu 1974: 151, pl. 66, figs 1–4), from the Shihtzupu Formation (early Caradoc) at Zunyi, Guizhou Province, differs from *irravadica* in having a smaller subquadrate shell, narrower divergent brachioophores (about 75° as compared with 90–110° in *irravadica*), much stronger peripheral crenulations and more developed dental plates. *Sulevorthis*, a small orthid named by Jaanusson & Bassett (1993: 40) with its type species *Orthis lyckholmiensis* Wysogórski from the Lyckholm Beds (Vormsi Stage, late Caradoc) of Kõrgessaare, Hiiumaa, Estonia, is very similar to *Saucrorthis* externally, but its strong cardinal process is elongate, occupies the entire notothyrial cavity and is separated from the brachioophores completely, and no notothyrial platform is developed.

Among all the species assigned to *Sulevorthis* by Jaanusson & Bassett (1993: 38), *Orthambonites parvicrassicosatus* (Cooper 1956: 309, pl. 35B, figs 11–25) from the Benbolt Formation (Porterfieldian, early Caradoc?) of Virginia, USA and *Orthambonites humilidorsatus* (Wright 1964: 160, pl. 1, figs 1–12) from the Portrane Limestone (Caradoc) of Ireland are the species of *Sulevorthis* most similar externally to our present material, particularly in the presence of exopunctae.

Family SKENIDIIDAE Kozłowski, 1929

Genus SKENIDIOIDES Schuchert & Cooper, 1931

Skenidioides sp.

?1936 *Skenidioides* cf. *billingsi* Schuchert & Cooper; Reed: 68, pl. 2, figs 8, 8a.

MATERIAL AND LOCALITY. One ventral valve (internal and external moulds), BB 37594, from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM 78), Southern Shan States.

DISCUSSION. A single broken shell 3.7 mm long and 4.7 mm wide, with radial costae branching only once within one-third of the shell length and 4 per mm on the shell anterior, a very high interarea and small teeth, is typical of *Skenidioides*. Reed described two species of this genus from the Southern Shan States, *Skenidioides* cf. *oelandicus* Wiman from the Naungkangyi Group at Nam Wabya (Reed 1936: 30, pl. 2, figs 18–21) and *Skenidioides* cf. *billingsi* Schuchert & Cooper from the Bawzaing Horizon (contemporary with the Naungkangyi Group) at Sinchaung (Reed 1936: 68, pl. 2, figs 8, 8a). *S. cf. oelandicus* does not appear from Reed's illustrations to be a *Skenidioides* because the ventral interarea is far too small. *S. cf. billingsi* is represented in Reed's material by a single ventral internal mould which may or may not be a *Skenidioides* and the same as the present specimen; it is poorly preserved.

Superfamily DALMANELLOIDEA Schuchert, 1913

Family DALMANELLIDAE Schuchert, 1913

Subfamily DALMANELLINAE Schuchert, 1913

Genus ONNIELLA Bancroft, 1928

Onniella chaungzonensis (Reed, 1906) Pl. 2, figs 6–10

1906 *Orthis* (*Dalmanella*?) *chaungzonensis* Reed: 61, pl. 4, figs 7–14.

1906 *Orthis* (*Dalmanella*) *testudinaria* Reed: 60, pl. 4, figs 25–26.

1915 *Orthis* (*Dalmanella*) *testudinaria shanensis* Reed: 9, pl. 2, figs 6–7, 9–10.

MATERIAL AND LOCALITIES. One dorsal and one ventral valve (both internal and external moulds) from the Naungkangyi Group in the Yadanatheingi area (Locality AM1); three dorsal valves (internal and external moulds), and five ventral internal and four external moulds from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Ta-Pangtawng (about 10 km east of Longtawno, Locality YA454.1), both in the Northern Shan States. One dorsal internal mould from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM77), Southern Shan States.

DESCRIPTION. *Exterior.* Small transverse shell 2.4–5.4mm long and 2.7–6.4mm wide with length/width ratio 0.75–0.89. Lateral profile unequally biconvex; gently convex dorsal valve with a conspicuous sulcus originating from the umbo, much deeper ventral valve with strongest convexity along the hinge line. Maximum width near the shell midlength. Ventral beak small; slightly curved apsacline interarea; open delthyrium; narrow anacline dorsal interarea; without chilidium but notothyrium occupied by strong cardinal process lobes (Pl. 2, fig. 10a). Ornament of densely populated costellae, branching medially and laterally on dorsal valve and laterally on ventral valve three times: firstly at one-quarter shell length, secondly at one-third length and finally at two-thirds length. No median rib on dorsal valve, but a deep and narrow groove along the median line with a pair of weak costellae on both sides starting at one-quarter of the shell length. Concentric growth lines dense and even over the whole shell. One or two stronger growth lines common near the anterior margin. Endopunctate shell.

Ventral interior. Strong teeth supported by a pair of subparallel, thick and short dental plates. Poorly impressed cordate muscle field about 30% of the length and width; slightly elevated central adductor scars not enclosed by diductor scars anteriorly. Strong crenulations near the margins of both valves about one-quarter of the length, which form broad, flat ridges separated by narrow deep grooves.

Dorsal interior. Strong and erect cardinal process limited to the posterior part of the notothyrial cavity, well-developed myophore fissured centrally. Robust brachioophores triangular at their bases and highly projecting mainly ventrally and slightly anteriorly; short and slightly divergent stout fulcral plates variably developed (strong in Pl. 2, fig. 10). No apparent notothyrial platform, but weak elevation of notothyrial cavity often developed. Well impressed rectangular muscle field just in front of the cardinalia, extending to more than 60% of the length and about 40% of the width, with low and wide bounding ridges and myophragm; two pairs of adductor scars, with the anterior pair of scars larger than the posterior pair. Low and wide median ridge extending to the anterior margin.

MEASUREMENTS

	L	W	L/W	L ₁	L ₂	W ₁	W ₂
BB37703, dorsal valve	5.2	5.8	0.89	0.9	—	1.3	—
BB37731, dorsal valve	5.4	6.3	0.86	1.4	3.1	2.0	2.5
BB37736, ventral valve	2.4	2.7	0.89	0.8	—	0.7	—
BB37738, dorsal valve	4.8	6.4	0.75	1.0	3.4	1.9	2.7

DISCUSSION. Bancroft (1928: 55) established *Onniella* for small dalmanellids with a transverse shell, small beaks, dorsal sulcus and no ventral pallial markings. Later (Bancroft, 1945: 211), he further summarized the main and distinguishing characters of *Onniella* as a small dalmanellid with *Resserella*-like crural plates, unequal-sized dorsal muscle scars, feebly-developed ventral muscle field, and without apparent pallial markings. According to Williams & Wright's (1963) detailed revision, *Dalmanella*, externally somewhat close to *Onniella*, differs from the latter in having small fulcral plates, convergent brachioophore supports, comparatively smaller dorsal muscle scars and a more elongate ventral muscle field. Hurst (1979) has discussed and redefined the various species of *Onniella* from the type Caradoc area of Shropshire, including *O. broeggeri* Bancroft, the type species. According to his convincing discussion, the differentiation of species within *Onniella* should be on ribbing and some aspects of the interiors, especially the shape of the ventral muscle field, rather than only on their ribbing patterns as Bancroft believed. The present material from Burma lacks fulcral plates in most specimens, has slightly divergent brachioophore supports, the ventral adductor scars are not enclosed by diductor scars and has rectangular

dorsal muscle fields with larger anterior pair of scars; it is therefore assigned to *Onniella*.

All the specimens identified as *Orthis* (*Dalmanella*?) *chaungzonensis* by Reed (1906: 61, pl. 4, figs 7–14) are from the Naungkangyi Group at Chaungzon, Northern Shan States, and have no essential differences from our material except for the equal-sized pairs of dorsal adductor scars shown in his figure 9, plate 4, which may have been overemphasised in Reed's drawing. The two exteriors identified as *Orthis* (*Dalmanella*) *testudinaria* by Reed (1906: 60, pl. 4, figs 25–26), from the same locality and horizon as *chaungzonensis*, have the same ribbing as the latter. *Orthis* (*Dalmanella*) *testudinaria shanensis* (Reed, 1915: 9, pl. 2, figs 6–11), from the Hwe Mawng Formation (equivalent to the Upper Naungkangyi Group) at Hkawnhkok, Northern Shan States, also has the same characters as *chaungzonensis*, except for two ventral interiors (Reed, 1915: pl. 2, figs 8, 11) which may be attributable to *Dalmanella* rather than *Onniella*, because the general shape of the ventral muscle field and the adductor and diductor scars are identical to that of the real *D. testudinaria* from the Baltic.

The *Orthis* (*Dalmanella*) *elegantula* of Reed (1906: 60, pl. 4, figs 23–24) was based on two distorted specimens from the Naungkangyi Group at Taungkyun, Northern Shan States, and differs from *chaungzonensis* in shell outline, ribbing and cardinalia but cannot be identified with certainty here. *Orthis* (*Dalmanella*) *sinchaungensis* (Reed 1936: 28, pl. 2, figs 12–15a) was named from the rocks corresponding to the Naungkangyi Group at Taungbu, Southern Shan States, and can be distinguished from *chaungzonensis* by much denser costellae, different ribbing style and a larger dorsal muscle field consisting of two pairs of equal-sized adductor scars, and may be a draboviid. The type species of *Onniella*, *O. broeggeri* (Bancroft 1928: 56, pl. 2, figs 1–5) from the Onny Shale Formation of Shropshire, differs from *chaungzonensis* in having coarser costellae and a smaller dorsal muscle field.

Superfamily **CLITAMBONITOIDEA** Winchell & Schuchert, 1893
Family **CLITAMBONITIDAE** Winchell & Schuchert, 1893

Indet. **clitambonitid**

Pl. 2, figs 11–12

MATERIAL AND LOCALITY. Four ventral internal and two external moulds from the Naungkangyi Group at Kunkaw (Locality YA40) in the Kyaukme-Longtawkno area, Northern Shan States.

DESCRIPTION. Transverse elliptical shell 5.1–10.2mm long and 7.0–13.8mm wide with length/width ratio 0.73–0.92. Variably convex ventral valve with a shallow and narrow sulcus originating in front of the umbo; apsacline interarea with a large and open delthyrium. Maximum width along the straight hinge line or slightly in front of it. Ornament of multicostellae, 3–4 per mm near the anterior margin. Teeth small; short and shallow spondylium supported by a weak median septum.

DISCUSSION. One of the ventral internal moulds is clearly a clitambonitid, based on the spondylium supported by the short median septum, but it is uncertain whether or not a pseudodeltidium or chilidium is present and thus to which subfamily it should be attributed. The *Clitambonites* cf. *squamata* Pahlen recognised by Reed (1906: 66, pl. 5, fig. 14), from the Naungkangyi Group at Kunlein, Northern Shan States, and the *Clitambonites* cf. *ascendens* Pander identified by Reed (1936: 31, pl. 3, fig. 14), from rocks corresponding to the Naungkangyi Group at Nam Wabya, Southern Shan States, are both based on single specimens which are very

similar to each other, as Reed himself recognised, and can probably be reassigned to *Porambonites* (see below). The ventral exterior identified by Reed (1906: 65, pl. 5, figs 13, 13a) as *Clitambonites* cf. *pyron* (Eichwald), also from the Naungkangyi Group at Sedaw (about 15 km northwest of Kyaukme), Northern Shan States, cannot be revised here owing to lack of material; it may or may not be a clitambonitoid.

Superfamily **PLECTAMBONITOIDEA** Jones, 1928

Family **LEPTELLINIDAE** Ulrich & Cooper, 1936

Subfamily **LEPTELLININAE** Ulrich & Cooper, 1936

Genus **LEPTELLINA** (*LEPTELLINA*) Ulrich & Cooper, 1936

Leptellina (*Leptellina*) *minor* sp. nov.

Pl. 2, figs 13–14; Pl. 3, figs 1–5

1936 *Leptelloidea* (*Leangella*?) cf. *derfelensis* Jones; Reed: 43, pl. 4, figs 24–25.

1936 *Leptelloidea* (*Leangella*) cf. *shoeshookensis* Jones; Reed: 43, pl. 4, fig. 28.

HOLOTYPE. BC 52418 (Pl. 3, fig. 2), from the equivalent of the Upper Naungkangyi Group at Linwe (AM78), Southern Shan States, longitude 96°33'E, latitude 21°14'N.

MATERIAL AND LOCALITIES. 107 specimens: 10 dorsal valves, 23 dorsal internal and 14 external moulds, four ventral valves, 33 ventral internal and 13 external moulds from the equivalents of the Upper Naungkangyi Group at Linwe (Localities AM77, AM78); moulds of two ventral interiors and one ventral exterior and counterpart interior from the Bryozoan Sandstone Formation (equivalent to the Upper Naungkangyi Group) in the Neyaungga-Ye-ngan area (Localities BA479, BA490); both in the Southern Shan States. Four ventral internal and two external moulds from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Ta-Pangtawng (about 10 km east of Longtawkn, Locality YA454.1), Northern Shan States.

DESCRIPTION. *Exterior.* Small semicircular shell 3.0–6.3 mm long and 3.4–8.4 mm wide, with length/width ratio 0.66–0.88. Lateral profile strongly concavo-convex, dorsal valve often dorsally geniculate at about 60% of length, strongly convex ventral valve particularly medially. Cardinal extremities acute to nearly rectangular; maximum width along the hinge line. Large, flat and apsacline ventral interarea; posterior half of the delthyrium covered by well-developed arched pseudodeltidium (Pl. 3, fig. 1a). Smaller anacline dorsal interarea; open notothyrium mostly occupied by cardinal process lobes. Parvicostellate ornamentat with 4–5 finer costellae between each pair of coarser ones. No growth lines observed.

Ventral interior. Small teeth with variably developed dental plates weak or absent and extending first subparallel and then medially to

enclose the muscle field. Delthyrial cavity very deep. Rectangular or transversely elliptical muscle field elevated from the shell floor, 17–27% of the length and 21–34% of the width; triangular median adductor scars often more elevated than the lateral diductor scars. Vascular markings lemniscate; a pair of strong vascular media originate from the antero-lateral ends of muscle field, extending forward subparallel and branching at about two-thirds of the length; a pair of very weak vascular spondylaria originate laterally from the muscle field, extending to the shell lateral margin with few branches.

Dorsal interior. Small transverse cardinalia 16–21% of the length and 28–31% of the width; strong median cardinal process lobe projecting posteriorly and ventrally and continuous with the low and wide myophragm anteriorly; small lateral pair of lobes variably developed, sometimes absent; socket ridges connected with cardinal process medially and extending laterally subparallel to the hinge line, with two strong ventrally projecting lateral ends; sockets transverse and elliptical. Poorly-impressed circular muscle field just in front of the cardinalia, antero-medial pair of adductor scars slightly larger than the lateral pair. Thin median septum starting from the posterior end of the inner adductor scars, becoming higher anteriorly and reaching its acme at the junction with the platform at the strongest valve convexity. Weakly-elevated platform composed of a series of continual or continuous tubercles, not connected with hinge line posteriorly. Lemniscate vascular markings with a pair of vascular media originating from the anterior ends of inner adductor scars.

MEASUREMENTS

	L	W	L/W	L ₁	L ₁ /L	W ₁	W ₁ /W
BB37590, dorsal valve	5.2	7.8	0.67	1.1	0.21	2.2	0.28
BB37625, dorsal valve	5.6	7.5	0.75	0.9	0.16	2.1	0.28
BB37635, ventral valve	4.6	6.1	0.75	1.2	0.26	2.1	0.34
BB37647, dorsal valve	4.4	5.8	0.76	0.8	0.18	1.8	0.31
BB37652, ventral valve	4.0	6.1	0.66	0.9	0.23	1.5	0.25
BB37742, ventral valve	3.0	3.4	0.88	0.5	0.17	0.8	0.24
BB37755, ventral valve	6.3	8.4	0.75	1.7	0.27	1.8	0.21

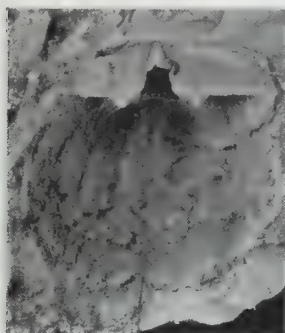
DISCUSSION. This species is the most abundant component of our fauna. Reed (1936: 43) identified a probably identical ventral interior as *Leptelloidea* (*Leangella*) cf. *shoeshookensis* Jones from rocks corresponding to the Naungkangyi Group at Taunggyi in the Southern Shan States. The true *Leptelloidea shoeshookensis* (Jones 1928: 488, pl. 15, fig. 19) has an undercut cardinal process and well-developed bema and platform, and has been reassigned to *Leangella* (*Leangella*) by Cocks & Rong (1989: 116). Reed also identified other specimens as *Leptelloidea* (*Leangella*?) cf. *derfelensis* Jones, but again that Welsh species has been reassigned to *Leangella* (*Leptestiina*) by Cocks & Rong (1989: 116). Reed illustrated no dorsal valves. Thus, with our more complete material than Reed, we can erect the new species *minor*, which we assign to *Leptellina* (*Leptellina*). It differs from the type species *L. tennesseensis* (named by Ulrich & Cooper in 1936: 626, but illustrated by Ulrich & Cooper in 1938: 192, pl. 39, figs 1–2, 4–5), from the Lenoir Formation

PLATE 3

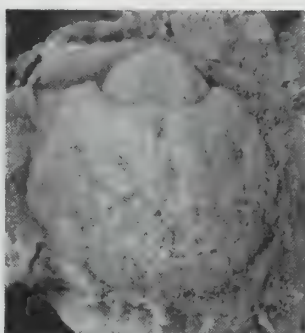
Figs 1–5 *Leptellina* (*Leptellina*) *minor* sp. nov. **1–4**, Linwe, Locality AM78. **1a, 1b**, BB 37623, latex cast and internal mould of ventral interior showing poorly developed pseudodeltidium and small teeth, $\times 5$. **2a, 2b**, BC 52418, Holotype, latex cast and internal mould of dorsal interior with another dorsal interior at the top left (BB 37590), $\times 5$. **3**, BB 37659, dorsal internal mould, $\times 4$. **4**, BB 37629, latex cast of dorsal exterior, showing dorsal interarea and chilidium, $\times 4$. **5**, BC 52417, Ta-Pangtawng, Locality YA454.1, ventral internal mould, $\times 6$.

Figs 6–9 *Bekkerella subcrateroides* (Reed). **6–8**, Kunkaw. **6**, BB 37768, Locality YA50.1, latex cast of dorsal exterior, $\times 4$. **7a–d**, BB 37759, Locality YA256, latex cast of exterior, internal mould, latex cast of interior and posterior view of internal mould of ventral valve together with a dorsal external mould (BC 52410), $\times 4$. **8a, 8b**, BB 37774, Locality YA315.1, dorsal internal mould, and latex cast, $\times 3$. **9a, 9b**, BB 37750, Namyun, latex cast and internal mould of dorsal interior, $\times 2$.

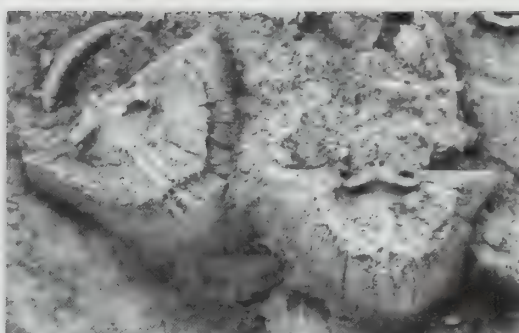
Fig. 10 *Ishimia subdeltoidea* (Reed). B 29672, Tawmawgon, latex cast and internal mould of dorsal interior, $\times 2$.



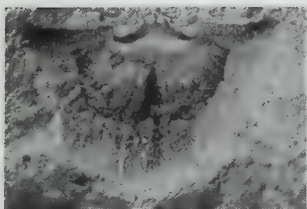
1a



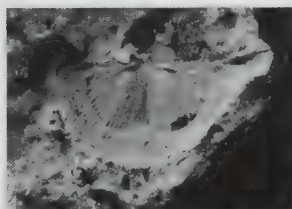
1b



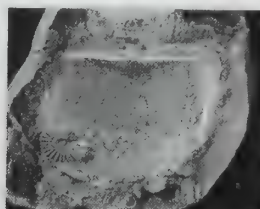
2a



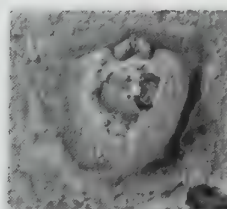
2b



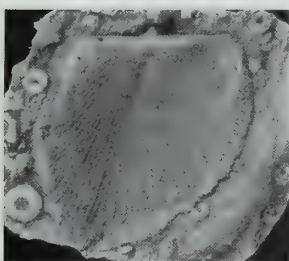
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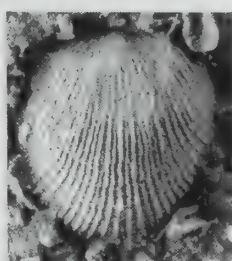
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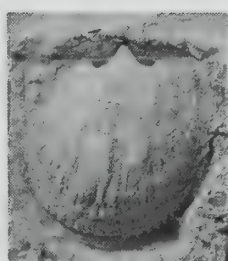
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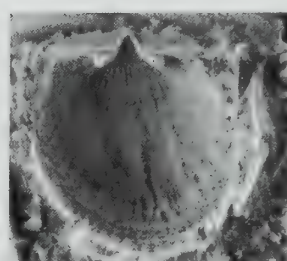
6



7a



7b



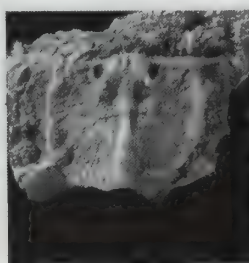
7c



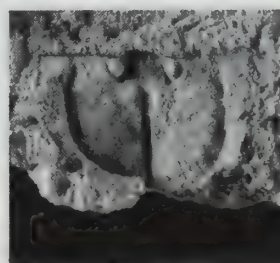
8a



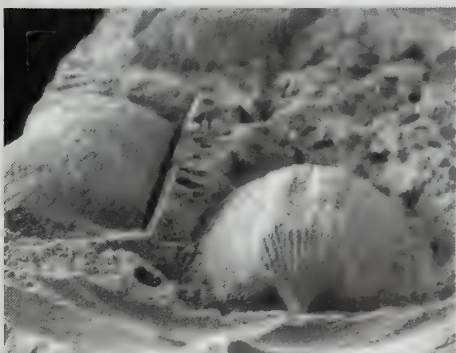
8b



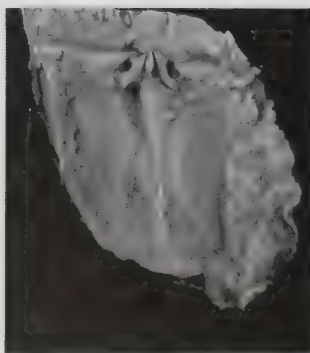
9a



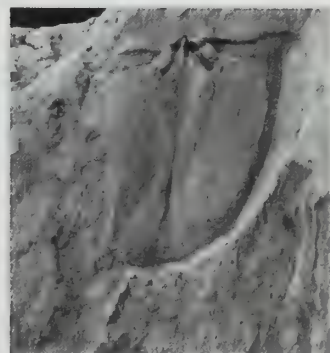
9b



7d



10a



10b

(Llandeilo) at Friendsville in Tennessee, U. S. A., in having a smaller shell, less numerous parvicostellae and less acute cardinal extremities. The *Leptellina sinensis* of Xu, Rong & Liu (1974: 152, pl. 66, figs 13, 17–18) from the Shihtzupu Formation (early Caradoc) of Guizhou, South China, differs from *minor* in having a much larger shell, comparatively larger dorsal interarea, denser parvicostellae, less well-developed ventral muscle field and dorsal platform.

The specimen identified by Reed (1915: 13, pl. 3, fig. 3) as *Plectambonites* cf. *llandeiloensis* (Davidson) from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Li-lu, Northern Shan States, has an undercut cardinal process, strongly elevated bema and well-developed platform, and is here reassigned to *Leangella* (*Leangella*) sp. Davidson's *llandeiloensis* itself has been reassigned to *Leptellina* by Williams (1962: 164). A ventral valve, the holotype of Reed's new species *Leptelloidea* (*Leangella*?) *lamellata* (1936: 44, pl. 4, figs 22–23, 23a), from rocks corresponding to the Naungkangyi Group at Taunggyi of the Southern Shan States, is similar to *L. (L.) minor* in shell outline and convexity, but differs from the latter in having fewer larger costellae, a more deeply impressed and more elongate muscle field and a pair of strong vascular dentalia. Since only a single ventral valve was illustrated, we consider *lamellata* as generically indeterminable. Comparably, *Leptelloidea yeosinensis* was described from Ye-o-sin, Southern Shan States, by Reed (1932: 196, pl. 3, figs 3–6) and the well-illustrated dorsal valves indicate that it is a leptellinid, but differing from *L. (L.) minor* in its lack of thin dorsal median septum anteriorly and the presence of a bema. However, its detailed generic position is not determinable.

Several variations are observed in our specimens of *L. (L.) minor*, including: (1) ventral convexity; most of the ventral valves are very convex but some are more gentle; (2) geniculation; over 80% of the dorsal valves have marked geniculation, while the remaining minority have much weaker or even absent geniculation; (3) ventral muscle field; the dental plates are usually weak and enclose the elevated muscle field in which the medial adductor scars are higher than the lateral diductor scars. Sometimes the small teeth have no supports and the slightly elevated diductor and adductor scars are indistinguishable from each other; (4) cardinal process; the central lobe is always well-developed, while the lateral lobes are often absent; (5) platform; the presence of a platform is one of the main characters of this genus, but it is variably developed and elevated in *L. (L.) minor*, and occasionally it is even composed merely of a series of discontinuous tubercles.

Genus *BEKKERELLA* Reed, 1936

Bekkerella subcrateroides (Reed, 1906) Pl. 3, figs 6–9

1906 *Orthis subcrateroides* Reed: 63, pl. 4, figs 27–33.

1915 *Orthis subcrateroides* Reed: Reed: 12.

1936 *Rafinesquina* (*Bekkerella*) *gentilis* Reed: 38, pl. 4, fig. 14.

MATERIAL AND LOCALITIES. Nine dorsal internal, eight external, 10 ventral internal and four external moulds from the Naungkangyi Group at Kunkaw (Localities YA42, YA50.1, YA256 and YA315.1); one dorsal internal, two external and four ventral external moulds from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Li-lu (about 11 km southeast of Longtawkno, Locality YA630); one ventral valve (internal and external moulds) from the Taungkyun Formation (equivalent to the Lower Naungkangyi Group) at Li-lu (Locality YA139); one ventral internal mould at Chaungzon, and two dorsal internal moulds at Namyun, both from the Naungkangyi Group; all in the Northern Shan States.

DESCRIPTION. *Exterior.* Subquadrate to subcircular shell 6.9–18.7 mm long and 7.7–23.8 mm wide with length/width ratio 0.71–1.0. Lateral profile concavo-convex; dorsal valve slightly concave medio-posteriorly with a small anterior geniculation; strongly convex ventral valve particularly medially. Cardinal extremities round, maximum width at about mid-length. Large flat apsacline ventral interarea, small beak, only posterior one-third covered by small arched pseudodeltidium; smaller hypercline dorsal interarea, notothyrium completely occupied by cardinal process. Multibranching costellae, equal in size, near the anterior margin, about 4 per mm. Growth lines closely spaced, 12 per mm longitudinally.

Ventral interior. Stout triangular teeth without supports. Delthyrial cavity with some secondary shell accumulation. Poorly-impressed muscle field about one-third to two-fifths of shell length and width, without apparent surrounding ridges, adductor and diductor scars indistinguishable from each other. Variably-developed subperipheral ridge extending posteriorly towards the hinge line and then medially to the teeth lateral sides parallel to the hinge line. Vascular markings saccate, a pair of vascular media originating in front of the muscle field and extending forward with several branches.

Dorsal interior. Small cardinalia 12–23% valve length and 21–32% valve width; cardinal process usually simple but occasionally trifid, median lobe elongate and strongly projecting ventrally and posteriorly; thick and straight socket ridges divergent at 60–100°, extending posteriorly and connecting with the lateral lobes of cardinal process; the whole notothyrial cavity highly elevated and thickened by secondary shell; large deep sockets open antero-laterally. Slightly elevated quadrate muscle field with distinctive bounding ridges, posterior pair of scars a little larger than the anterior pair; thick and strong myophragm originating from the notothyrial platform, becoming thinner and higher anteriorly, with its acme just in front of the muscle field, merging into the platform. Variably-developed quadrate platform slightly undercut and extending posteriorly to the hinge line. All the area outside the platform geniculate dorsally.

MEASUREMENTS

	L	W	L/W	L1	L1/L	W1	W1/W	∞
BC52182, dorsal valve	6.9	7.7	0.90	1.3	0.19	2.1	0.27	75°
BB37750, dorsal valve	11.5	16.1	0.71	2.6	0.23	3.6	0.22	60°
BB37757, dorsal valve	18.7	23.8	0.79	2.3	0.12	5.0	0.21	100°
BB37759, ventral valve	8.7	8.7	1.0	2.9	0.33	2.9	0.33	–
BB37774, dorsal valve	8.6	10.4	0.83	1.6	0.19	3.3	0.32	89°
SMA3128, ventral valve	11.9	12.3	0.97	5.2	0.44	5.0	0.41	–

DISCUSSION. *Bekkerella* appears endemic to Burma and is characterized by undifferentiated fine radial ornamentation, a slightly elevated and distinctive dorsal muscle field, a strong median septum and a quadrate platform. *Acculina* and *Shlyginia*, also common in Caradoc times, are similar to *Bekkerella* in dorsal interior, but they both have parvicostellate ornamentation, and in addition *Acculina* has a resupinate profile, well-developed pseudodeltidium and a bilobed ventral muscle field with extended dental plates as bounding ridges (Cocks & Rong 1989: 103). *Shlyginia* has a much larger ventral muscle field within which adductor scars are enclosed by diductor scars, and a small cardinal process seldom projecting posterior to the hinge line.

Reed (1936: 38) erected the subgenus *Bekkerella* within *Rafinesquina*, with *Orthis subcrateroides* Reed (1906) from the Naungkangyi Group at Chaungzon in the Northern Shan States as its type species. The single ventral interior which he illustrated from the Southern Shan States in 1936 has a muscle field which was overemphasised in the drawing (Reed 1936, pl. 4, fig. 14), since none of

Reed's illustrated ventral valve muscle fields of *subcrateroides* is so elongate and divergent. All our present specimens are also from the Naungkangyi Group from several localities in the Northern Shan States and are identical to *subcrateroides*. Some variations observed in this material are: (1) dorsal concavity; most dorsal valves are slightly concave or nearly flat medial-posteriorly, with a small but strong geniculation anterior to the platform, but there are a few individuals with an evenly concave dorsal valve and no geniculation (e.g. Pl. 3, fig. 6); (2) cardinal process; lateral lobes are usually absent, but they are present in a few specimens and continuous antero-laterally with the straight socket ridges; (3) platform; most dorsal valves have a well-developed and slightly undercut platform, but a few specimens, particularly juveniles, have a very weak platform.

Subfamily **PALAEOSTROPHOMENINAE** Cocks & Rong, 1989

Genus **ISHIMIA** Nikitin, 1974

Ishimia subdeltoidea (Reed, 1906)

Pl. 3, fig. 10; Pl. 4, figs 1–7

1906 *Rafinesquina subdeltoidea* Reed: 52–53, pl. 5, figs 1–8.

1936 *Rafinesquina* (*Kjaerina*) cf. *felix* Reed; Reed: 37, pl. 4, fig. 1.

MATERIAL AND LOCALITIES. Eight dorsal internal, six external, eight ventral internal and three external moulds at Tawmawgon (about 30 km north of Kyaukme); three dorsal internal, one ventral internal and one external moulds at Kunkaw (Localities YA45.1, YA315), both from the Naungkangyi Group; two dorsal internal and external moulds from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Ta-Pangtawng (about 10 km east of Longtawkn); all in the Northern Shan States. Two dorsal internal moulds from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM77), Southern Shan States.

TYPES. Lectotype, here selected, the original of Reed 1906, pl. 5, fig. 4, a dorsal internal mould from Tawmawgon, Northern Shan States. Indian Geological Survey Museum, Calcutta.

DESCRIPTION. *Exterior.* Lateral profile concavo-convex; dorsal valve flat or slightly concave medial-posteriorly, with variably developed dorsal geniculation, some strong and nearly perpendicular; ventral valve convex, with convexity increasing anterior to the dorsal valve geniculation. Cardinal extremities usually acute, maximum width along the hinge line. Large, apsacline, flat ventral interarea; ventral beak slightly curved; delthyrium only about one-quarter covered by pseudodeltidium. Smaller hypercline dorsal interarea with a well-developed arched chilidium. Ornament of coarse parvicostellae, unevenly distributed, about 3–4 per mm near the margin; only 1–2 finer costellae between two coarser ones. Growth lines well-preserved on the geniculation, 8–9 per mm; several concentric comae often present postero-laterally.

Ventral interior. Small triangular or wedge-like teeth without supports. Weakly-impressed muscle field with no bounding ridges; antero-medial pair of diductor scars much larger than the postero-lateral pair and with a short and weak myophragm, small adductor scars in the posterior centre of the muscle field. Vascular markings lemniscate; vascular media originating from the inner sides of the anterior end of the muscle field, and vascular myaria starting between the two pairs of diductor scars.

Dorsal interior. Cardinalia about one-fourth shell length and width; very high, thin plate-like cardinal process median lobe pro-

jecting ventrally, lateral lobes often absent; straight socket ridges separated from the median lobe, divergent at about 75–100°, extending antero-laterally far beyond the sockets, showing thin plate-like crura; the cardinal area elevated by the deposition of secondary shell; deep and narrow or round sockets open or with thick and low bounding ridges antero-laterally. Well-impressed elongate oval muscle field including a smaller anterior pair and larger posterior pair of adductor scars, low bounding ridges often absent; thick and high myophragm originating from the notothyrial platform and extending forward to become thinner and higher, reaching its acme at the anterior end of the muscle field and continuous anteriorly with the thin median septum which ends before or merges into the platform. Quadrate platform slightly elevated, extending posteriorly to the hinge line. The geniculation is immediately anterior of the platform.

DISCUSSION. Most of our present material was collected from Reed's type locality of *subdeltoidea*, Tawmawgon in the Northern Shan States, and is identical to Reed's illustrated specimens. The distorted dorsal interior, from rocks corresponding to the Naungkangyi Group at Hpungyi Kyau in the Southern Shan States and identified by Reed as *Rafinesquina* (*Kjaerina*) cf. *felix*, is basically similar to some of our specimens and is thus assigned to *subdeltoidea* here. The true *felix* of Reed (1917) is a quite different strophomenoid from the middle Ashgill of Girvan, Scotland (Cocks 1978). When Nikitin (1974: 59) established *Ishimia* from the Middle Ordovician of Central Kazakhstan, he recognised four species, *I. humilis* (Nikitin 1974: 63; pl. 6, figs 1–3), from the Yerkebidai Horizon (middle Caradoc) of Chingiz in Central Kazakhstan, lacks geniculation, but otherwise is the most similar to *subdeltoidea*, although it differs in having finer costellae and a more elongate bilobed ventral muscle field. The type species, *I. ishimensis* (Nikitin 1974: 61, pl. 5, figs 10–16) from the Karakan Horizon (late Llanvirn) of Kupriyanovka in Central Kazakhstan, can be distinguished in having finer and more differentiated costellae, larger ventral adductor scars, and stronger dorsal bounding ridges, median septum and platform.

Some variations within the dorsal interior observed from our material of *I. subdeltoidea* are: (1) cardinal process; most specimens have only a strong single cardinal process lobe, but a few develop a pair of small lateral lobes, making the cardinal process trifid and hence the genus is appropriately placed within the Leptellinidae; (2) sockets; the antero-lateral sides are sometimes open, while a few specimens have low bounding ridges; (3) median septum; this usually ends before the platform, but in a few specimens it merges anteriorly with the platform.

Family **SOWERBYELLIDAE** Öpik, 1930

Subfamily **PTYCHOGLYPTINAE** Cooper, 1956

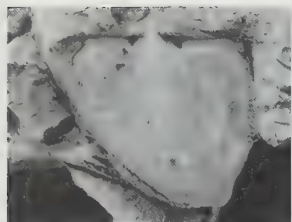
Genus **PTYCHOGLYPTUS** Willard, 1928

Ptychoglyptus? shanensis Reed, 1932

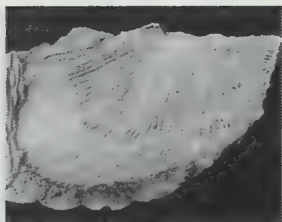
1932 *Ptychoglyptus shanensis* Reed: 195, pl. 3, fig. 15.

1936 *Ptychoglyptus shanensis* Reed; Reed: 37.

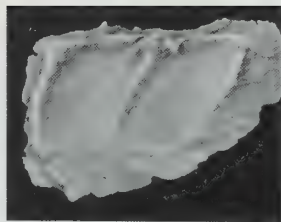
DISCUSSION. Reed (1932) named the species *Ptychoglyptus shanensis* from rocks corresponding to the Naungkangyi Group at Ye-o-sin in the Southern Shan States, on the basis of a single specimen showing distinctive zigzag rugae interrupted by costae. Although it may be a *Ptychoglyptus*, this is not certain until interiors are discovered, since very similar ornament can be found on some strophomenoid rafinesquids such as *Pentlandina*. Thus the generic attribution is queried here.



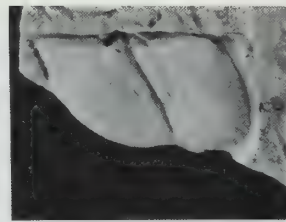
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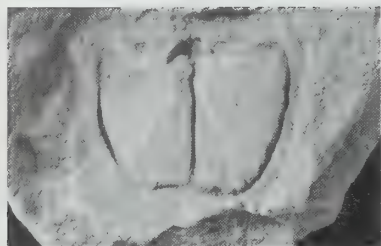
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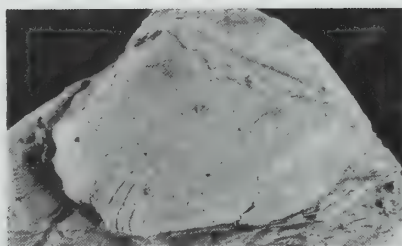
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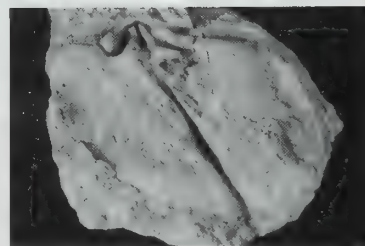
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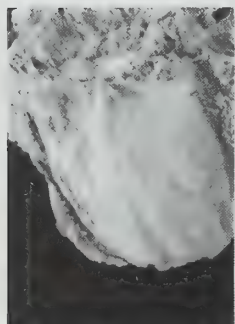
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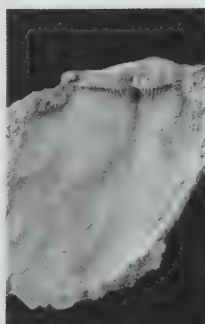
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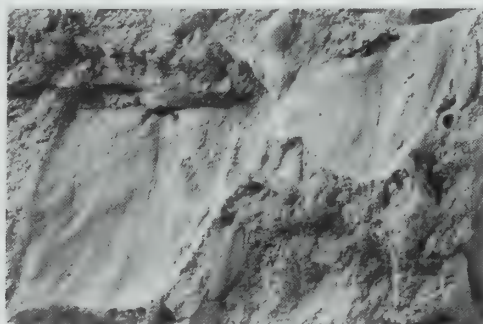
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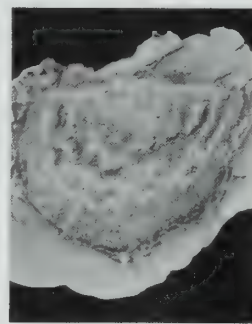
7a



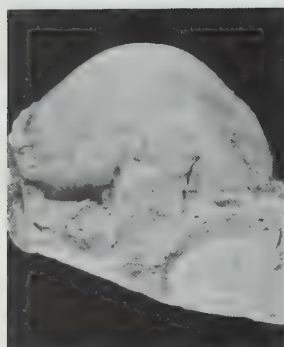
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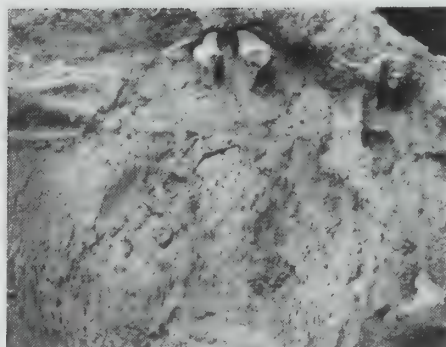
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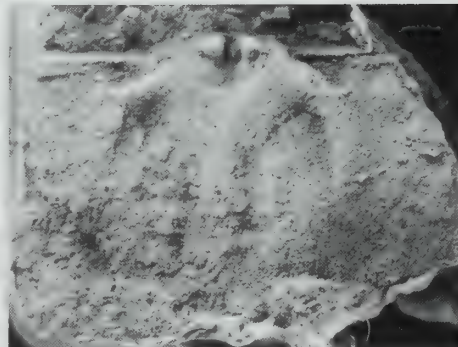
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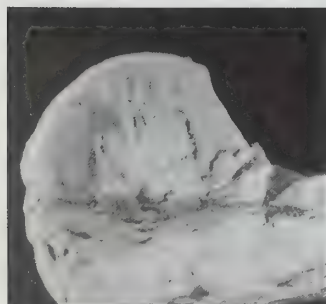
9a



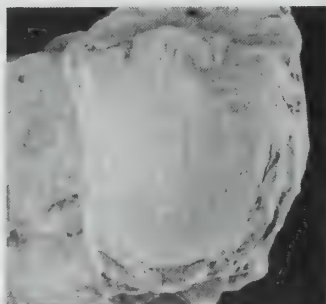
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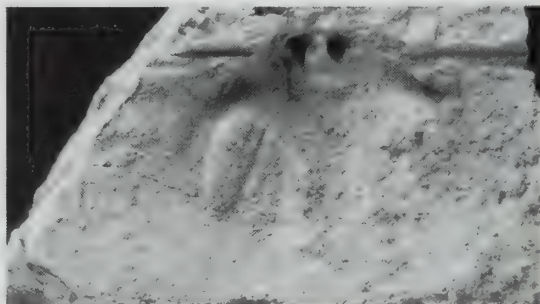
11a



9b



9c



11b

Superfamily **STROPHOMENOIDEA** King, 1846

Family **STROPHOMENIDAE** King, 1846

Subfamily **FURCITELLINAE** Williams, in Williams *et al.*, 1965

Genus **BELLIMURINA** (*BELLIMURINA*) Cooper, 1956

Bellimurina (*Bellimurina*)? sp.

Pl. 4, fig. 8

DISCUSSION. One ventral valve (internal and external moulds, BB37585) from the equivalents of the Upper Naungkangyi Group at Linwe, Southern Shan States, has some characters typical of *Bellimurina* (*Bellimurina*), such as a convex ventral valve with dorsal geniculation, a surface covered by zigzag rugae, and short and divergent dental plates (Cooper 1956: 854); but lack of material, especially dorsal valves, still makes our identification uncertain. *Bellimurina rudis* Xu, Rong & Liu (1974: 153, pl. 66, figs 14–16), from the Shihtzupu Formation (early Caradoc) of northern Guizhou, South China, is larger in shell size, has much stronger zigzag rugae and more impressed ventral muscle field with distinctive surrounding ridges. It is therefore not conspecific with this Burmese specimen.

Family **RAFINESQUINIDAE** Schuchert, 1893

Subfamily **RAFINESQUININAE** Schuchert, 1893

Genus **DIRAFINESQUINA** gen. nov.

TYPE SPECIES. *Dirafinesquina globosa* sp. nov.

DIAGNOSIS. Family characteristics of Rafinesquinidae. Like *Rafinesquina* but with ventral valve bounding ridges surrounding a suboval muscle field; cardinal process lobes weaker and erect rather than anteriorly directed and with socket ridges better developed.

DESCRIPTION. As for *Dirafinesquina globosa* below.

DISCUSSION. The true *Rafinesquina*, from the Caradoc-Ashgill of North America, has been revised and reillustrated by Rong & Cocks (1994). Reed (1906, 1936) attributed various Burmese specimens to species of *Rafinesquina* (see specific discussion below), but we consider that all the specimens in our collections and some of Reed's material from the Shan States may be grouped together within a single species, erected below as *Dirafinesquina globosa*.

The new genus can be firmly placed within the subfamily Rafinesquininae and the family Rafinesquinidae by its cardinalia, normal convexity and lack of rugae. There are ten other members of the subfamily. Of those of comparable age, *Rafinesquina* itself appears the closest, but with the differences mentioned in the diagnosis above. *Dirafinesquina* differs from *Colaptomena* and *Hedstroemina* in the large chilidium and pseudodeltidium and from the former in the lack of dorsal median septum; and from the latter in the lack of strong dental plates. It differs from *Kjaerina* in the suboval rather than triangular ventral muscle field and larger

chilidium, and from *Kjerulfina* in its lack of ventral geniculation and rugae. *Megamyonia* has distinctive ventral trans-muscle septa and other very different characters. *Odoratus* has ventral geniculation and lacks ventral muscle bounding ridges. *Rhipidomena* is resupinate and has dorsal trans-muscle ridges.

Dirafinesquina globosa sp. nov.

Pl. 4, figs 9–11; Pl. 5, figs 1–3, 5

?1936 *Rafinesquina* cf. *alternata* Conrad; Reed: 69, pl. 3, fig. 6.

1936 *Rafinesquina* cf. *semiglobosina* Davidson; Reed: 70, pl. 3, fig. 7.

HOLOTYPE. BB37593 (Pl. 4, fig. 11), from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM78), Southern Shan States, longitude 96°33'E, latitude 21°14'N.

MATERIAL AND LOCALITIES. 31 specimens: three dorsal internal and two external, 20 ventral internal and six external moulds from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM78) and Loke-pyin (about 14 km southeast of Ye-ngan, Locality AM106), Southern Shan States.

DESCRIPTION. *Exterior.* Large, subcircular shell more than 20mm long and wide with length/width ratio about 1.0. Lateral profile concavo-convex; dorsal valve evenly and gently concave; ventral valve gently convex posteriorly, with variable but sometimes sharply increasing convexity dorsally at about mid-length. Cardinal extremities round or rectangular, maximum width along the hinge line or a little anterior to it. Large flat apsacline ventral interarea with an arched pseudodeltidium, narrower anacline dorsal interarea with a much larger and more arched chilidium. Ornament of multibranching parvicostellae, 3–5 finer costellae between two coarser ones. No growth lines observed.

Ventral interior. Small rod-like or triangular teeth supported by weak dental plates which extend forward as muscle bounding ridges. Well-impressed, elongated oval muscle field 43–55% valve length and 37–39% valve width; a pair of long, kidney-shaped adductor scars slightly elevated and open anteriorly; diductor scars narrowing anteriorly, but longer than the adductor scars. Saccate vascular markings with a pair of vascular media originating from the anterior ends of adductor scars.

Dorsal interior. Relatively small cardinalia (Type B of Rong & Cocks 1994) with a variably developed, sometimes ponderous, cardinal process; triangular, sessile and discrete lobes including a plate-like shaft and a swollen myophore, and project ventrally and anteriorly; low, short, straight and variably thick socket ridges separated from the cardinal process; notothyrial cavity elevated; small shallow sockets open antero-laterally. Well-impressed circular muscle field, particularly posteriorly; low and wide myophragm starting from the notothyrial platform and narrowing anteriorly. No vascular markings observed.

MEASUREMENTS. Most of our specimens are broken and so only

PLATE 4

Figs 1–7 *Ishimia subdeltoidea* (Reed). Tawmawgon. **1**, BC 52420, ventral internal mould, $\times 1.5$. **2**, SMA 3124, latex cast of ventral exterior, $\times 1.5$. **3a, 3b**, SMA 3127, latex cast and internal mould of dorsal interior, $\times 1.5$. **4**, SMA 3126, dorsal internal mould, $\times 2$. **5**, SMA 3125, dorsal external mould, oblique view showing the dorsal geniculation, $\times 1.5$. **6**, BC 52191, dorsal internal mould showing small curved socket ridges, $\times 2$. **7a–c**, B 29664, latex cast and internal mould of a dorsal valve with another dorsal internal mould to the right, both with weaker platforms, $\times 1.5$.

Fig. 8 *Bellimurina* (*Bellimurina*)? sp. BB 37585, Linwe, Locality AM78, latex cast of ventral exterior, $\times 4$.

Figs 9–11 *Dirafinesquina globosa* gen. et sp. nov. Linwe, Locality AM78. **9a–c**, BB 37607, lateral, posterior and ventral views of ventral internal mould, $\times 1.5$. **10**, BB 37600, latex cast of dorsal interior showing the cardinalia and muscle field, $\times 5$. **11a, 11b**, BB 37593, Holotype, latex cast and internal mould of dorsal interior, $\times 5$.

three ventral valves are measured here.

	L	W	L/W	L1	L1/L	W1	W1/W
BB37606, ventral valve	23.9	23.7	1.01	13.2	0.55	9.2	0.39
BB37607, ventral valve	23.7	23.6	1.00	10.8	0.46	8.8	0.37
BB37619, ventral valve	20.6	20.5	1.00	8.9	0.43	7.8	0.38

DISCUSSION. A dorsal valve (Reed 1936: 69, pl. 3, fig. 6) was identified as *Rafinesquina* cf. *alternata* Conrad and a ventral valve (Reed 1936: 70, pl. 3, fig. 7) identified as *R.* cf. *semiglobosina* Davidson; both were from the Bawzaing Horizon (equivalent to the Naungkangyi Group) of Sinchaung, Southern Shan States: both are similar to our present material. *R. alternata*, the type species of *Rafinesquina* from the Hudson River Group (Caradoc) at Cincinnati, Ohio, U. S. A., differs from the Burmese material in having a larger shell, much less differentiated but denser costellae, and less impressed ventral muscle field, as well as the generic differences mentioned above. The true *semiglobosina* (see Reed 1917: 869, pl. 12, figs 13–20) has cardinalia of Type A and well-developed dorsal transmuscle ridges and has been reassigned to the furcitellid *Dactylogonia* by Williams (1962: 201) and Cocks (1978: 120). So we propose a new species *globosa* for our specimens, in which we provisionally include Reed's two exteriors.

The specimens illustrated as *Rafinesquina imbrex* Pander by Reed (1906: 52, pl. 5, figs 9–12), from the Naungkangyi Group at Tawmawgon in the Northern Shan States, have cardinalia of Type A, well-developed dorsal muscle-bounding ridges and a strong median septum, and so they are within the subfamily Furcitellinae. The dorsal exterior identified as *Rafinesquina* cf. *richardsoni* Reed by Reed (1936: 37, pl. 3, fig. 9), from the rocks corresponding to the Naungkangyi Group at Hpongyi Kyaung in the Southern Shan States, differs from our new species in having a much more transverse shell and denser costellae. Compared with the true *richardsoni* (Reed 1917: 868, pl. 12, figs 11, 11a, 12) from the Whitehouse Group (Caradoc) at Shalloch Mill, Girvan, its ornament is more differentiated and denser, although they are similar in shell outline. Since no internal moulds are available, the specimen has not been reidentified here.

Subfamily LEPTAENINAE Hall & Clarke, 1894

Indet. leptaeinines

Pl. 5, fig. 4

DISCUSSION. One exterior (BB37744), from the Li-lu Formation (equivalent to the Upper Naungkangyi Group) at Ta-Pangtawng (about 10 km east of Longtawko), Northern Shan States, has well-differentiated parvicostellae with 6–8 finer costellae between two coarser ones, evenly populated growth lines 18 per mm, and concentric rugae, and appears to be a leptaeinine. Two specimens from the Naungkangyi Group at Ledet and Lebyaungbyan (about 7 km west of Maymyo), Northern Shan States, identified by Reed (1906: 55, pl. 4, figs 39–41) as the new species *Leptaena*? *ledetensis*, have stronger

and fewer coarse costellae which cut through all the concentric rugae, and a distinctive ventral interior, so *ledetensis* should probably be reassigned to some other genus, possibly outside the Rafinesquinidae. Reed (1936) also identified three species of *Leptaena*, all on the basis of single specimens from rocks corresponding to the Naungkangyi Group in the Southern Shan States. The specimen Reed (1936: 33, pl. 3, fig. 3) called *L.* cf. *juvenilis* Öpik has undifferentiated costellae and strong concentric rugae which bend suddenly posteriorly at a sharp re-entrant angle in the valve centre, but the true *juvenilis* from Estonia (Öpik 1930: 173, pl. 11, figs 140–141; pl. 12, figs 142–145) has parvicostellae and concentric rugae not bending in the middle: however, Reed's Burmese specimen might be assigned to *Leptaena* (*Leptaena*). The *Leptaena* cf. *richmondensis* Foerste of Reed (1936: 34, pl. 3, fig. 11) is a ventral valve which is different from Foerste's true *richmondensis* (1909: 211, pl. 4, figs 10A, B) from the Waynesville Formation of Madison, Indiana, U.S.A., in having a different shell outline, well-differentiated parvicostellae and less developed concentric rugae. We also assign it to *Leptaena* (*Leptaena*), but it is not certain whether or not the various Burmese specimens belong to the same species. *Leptaena spectata* Reed (1936: 34, pl. 3, fig. 12), from the Naungkangyi Group of Taungtala, Southern Shan States, is founded on a single distorted ventral internal mould although it is similar to our specimen in ornamentation; but we cannot properly characterise Reed's species without more material, and thus leave the one or more leptaeinine species from the Naungkangyi Group in open nomenclature.

Family GLYPTOMENIDAE Williams, in Williams *et al.*, 1965

Subfamily GLYPTOMENINAE Williams, in Williams *et al.*, 1965

Genus GLYPTOMENA Cooper, 1956

Glyptomena sp.

Pl. 5, fig. 6

DISCUSSION. A single concave dorsal valve (external and internal mould, BB37586), from the equivalents of the Upper Naungkangyi Group at Linwe (Locality AM78), Southern Shan States, has a pair of small, discrete and sessile cardinal process lobes with straight socket ridges fused directly onto their lateral bases, which is typical of *Glyptomena*. Little can be seen on the external and internal moulds except for the cardinalia.

Superfamily PORAMBONITOIDEA Davidson, 1853

Family SYNTROPHOPSIDAE Ulrich & Cooper, 1936

Indet. syntrophopsid

Pl. 5, fig. 7

DISCUSSION. One slightly distorted ventral valve (BB37691), from the equivalents of the Upper Naungkangyi Group at Loke-pyin (about 14 km southeast of Ye-ngan, Locality AM106), Southern

PLATE 5

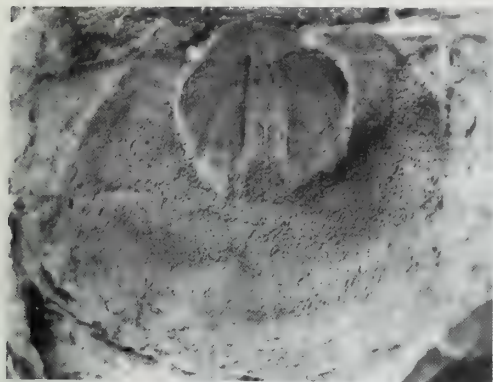
Figs 1–3, 5 *Dirafinesquina globosa* gen. et sp. nov. Linwe, Locality AM78. **1a–d**, BB 37619, latex cast, and anterior, ventral and posterior views of ventral internal mould, $\times 2$. **2a, 2b**, BB 37606, posterior and ventral views of ventral internal mould, $\times 1.5$. **3**, BB 37612, ventral internal mould, $\times 5$. **5**, BB 37604, ventral internal mould, showing the muscle field, $\times 2$.

Fig. 4 Indeterminate leptaeinid. BB 37744, Ta-Pangtawng, Locality YA454.1, latex cast of dorsal exterior, $\times 2$.

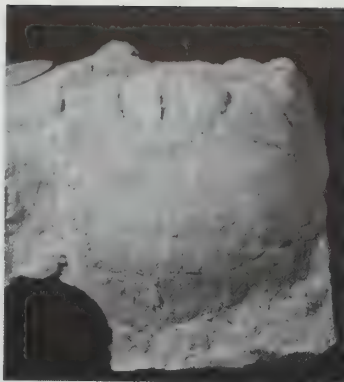
Fig. 6 *Glyptomena* sp. BB 37586, Linwe, Locality AM78, **6a–c**, latex cast and internal mould of dorsal interior, and dorsal external mould, $\times 3$, $\times 2$, $\times 2$.

Fig. 7 Indeterminate syntrophopsid. BB 37691, Loke-pyin, Locality AM106, latex cast and internal mould of ventral interior, $\times 5$, $\times 10$.

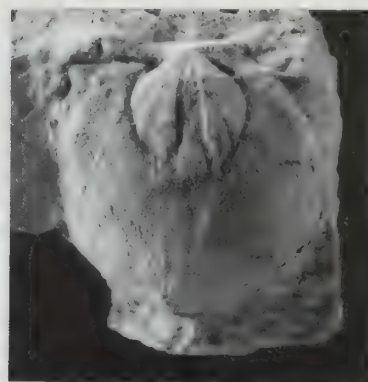
Figs 8–9 *Porambonites* spp. **8**, B 29671, Lebyaungbyan, ventral internal mould, $\times 1.5$. **9a, 9b**, SMA 3133, Sedaw, ventral and dorsal views of conjoined valves, $\times 1.5$.



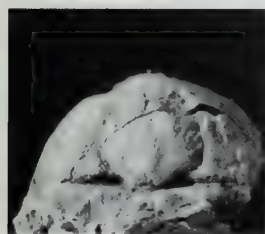
1a



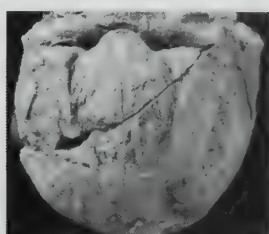
1b



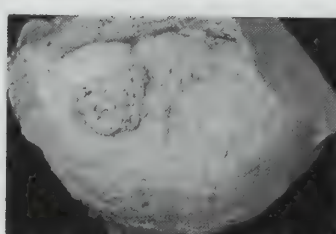
1c



2a



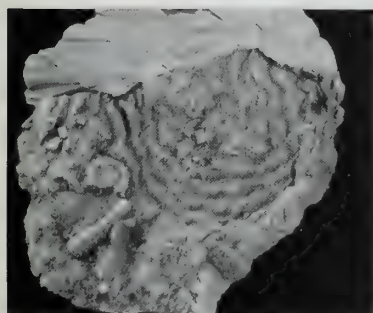
2b



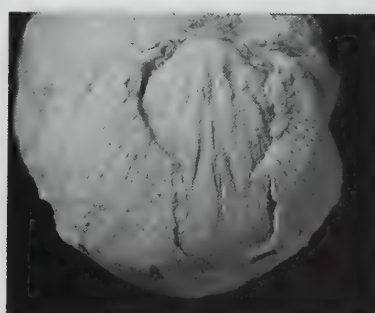
3



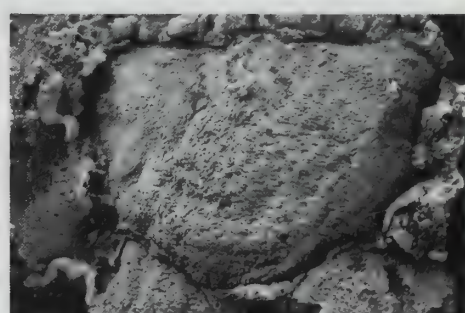
1d



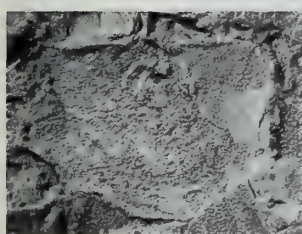
4



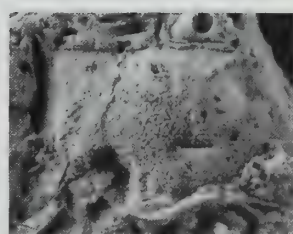
5



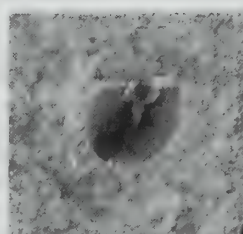
6a



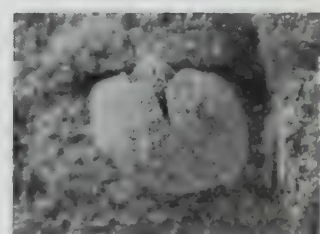
6b



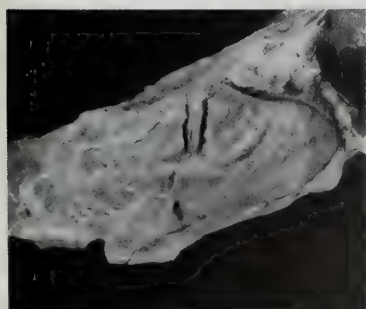
6c



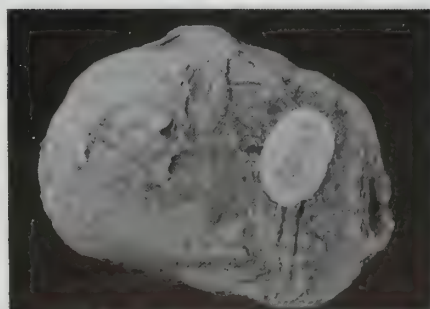
7a



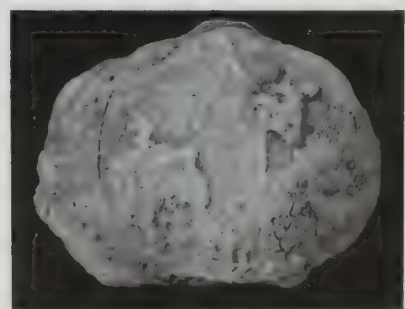
7b



8



9a



9b

Shan States, has a smooth shell, a mostly sessile spondylium and a short median septum originating near the anterior end of the spondylium, all of which are typical of *Syntrophopsis* Ulrich & Cooper (1936: 630). Among the 12 species recognized by Ulrich & Cooper (1938) within *Syntrophopsis*, *S. laevicula* (p. 233, pl. 50, figs 22–28), from the West Spring Creek Formation (late Arenig) of Oklahoma, U. S. A., is most similar to our specimen, but without more material, particularly the dorsal interior, no further identification is possible.

Family **PORAMBONITIDAE** Davidson, 1853

Genus **PORAMBONITES** Pander, 1830

Porambonites spp.

Pl. 5, figs 8–9

MATERIAL AND LOCALITIES. One individual, SMA 3133, with conjoined valves from Sedaw (about 15 km northwest of Kyaukme) and one ventral internal mould, B 29671, from Lebyaungbyan (about 7 km west of Maymyo), both from the Naungkangyi Group of the Northern Shan States.

DESCRIPTION. Subquadrate dorsi-biconvex shell. Straight hinge line about two-thirds of shell width, round cardinal extremities; maximum width at mid-length. Dorsal fold originating from the umbo; ventral sulcus starting at about mid-length and widening anteriorly to two-thirds shell width. Uniform costellae 4 per mm near the anterior margin. Thin, high and subparallel dental plates to about 40% of shell length; a low transverse ridge connecting their two anterior ends forming a sessile pseudospondylium.

DISCUSSION. Williams *et al.* (1965: H532) accepted *P. intermedius* Pander (1830) as the nominate type species but pointed out that *P. reticulatus* Pander (1830) represents the distinctive characters of this genus. The specimens from Burma have some crucial features of *Porambonites*, i.e., the outline, sulcus and the sessile pseudospondylium in one specimen. The individual illustrated and recognised by Reed (1906: 68, pl. 5, figs 15, 15a, 15b) as *P. intercedens* Pander, from the same locality and horizon as ours, has a globular outline, weaker fold and sulcus, and denser radial ornamentation. *P. sinuatus* Reed (1915: 14, pl. 3, figs 4–5), named on the basis of a ventral valve from the Upper Naungkangyi Group at Mangai of the Northern Shan States, has a much deeper sulcus and a pair of divergent dental plates. Reed (1936) also recognised two species from rocks corresponding to the Naungkangyi Group in the Southern Shan States. *P. cf. acutiplicata* Reed from Konleau (Reed 1936: 48, pl. 3, figs 1–2) has a much more transverse shell with comparatively shorter hinge line and deeper sulcus originating from the umbo and might also be referred to *Porambonites* sp. The true *acutiplicata* Reed (1917: 68, pl. 22, figs 10–11) from Girvan, Scotland, is more circular with a longer hinge line. *P. cf. wahl*i Heinrichson from Ye-o-sin (Reed 1936: 49, pl. 3, fig. 15) has a more circular shell, a weaker fold and much denser costellae, which is very similar to Heinrichson's true *wahl*i (1932: 159, pl. 2, figs 1–4) from the Caradoc of Estonia, so Reed's identification is suitable in the absence of more material. Specimens of *P. triquetrus* Xu, Rong & Liu (1974: 153, pl. 66, figs 34–35) from the Shihtzupu Formation (early Caradoc) at Zunyi, Guizhou, South China, are very similar to our material except for their shorter hinge line and weaker fold and sulcus. As mentioned under the indeterminate clitambonitid above, the two specimens illustrated as *Clitambonites cf. squamata* by Reed (1906: 66, pl. 5, fig. 14) and *Clitambonites cf. ascendens* by Reed (1936: 31, pl. 3, fig. 14) may also represent a species of

Porambonites, but it appears to be a different species from our illustrated specimens and also from *P. sinuatus*. In summary, there are not enough Naungkangyi specimens of *Porambonites* to identify the species with confidence, and it appears that there may be three or even more different species in our material.

Superfamily **LISSATRYPOIDEA** Twenhofel, 1914

Family **PROTOZYGIDAE** Hall & Clarke, 1893

Subfamily **PROTOZYGINAE** Hall & Clarke, 1893

Genus **PROTOZYGA** Hall & Clarke, 1893

Protozyga? haydeni Reed, 1936

1936 *Protozyga haydeni* Reed: 51, pl. 4, fig. 12.

DISCUSSION. Although there are no atrypoids in our new material, a distinctive dorsal valve from rocks corresponding to the Naungkangyi Group at Taunggyi in the Southern Shan States, was illustrated by Reed (1936: 51) as *Protozyga haydeni*. This was reassessed by Copper (1986: 834) as *P.? haydeni* Reed and we agree. In addition, Reed also figured a single pair of external moulds (1936: 52, pl. 5, figs 9–10) from the same locality and horizon as *P.? haydeni* which he identified as *Protozyga? cf. obsoleta* Foerste, but which we consider unidentifiable.

Subfamily **CYCLOSPIRINAE** Schuchert, 1913

Genus **CYCLOSPIRA** Hall & Clarke, 1893

Cyclospira sp.

?1932 *Hyattidina* sp. Reed: 206, pl. 3, figs 17–18.

1936 *Cyclospira? sp.* Reed: 52, pl. 4, fig. 13.

DISCUSSION. Reed (1936) figured a ventral valve as *Cyclospira? sp.* from rocks corresponding to the Naungkangyi Group at Taunggyi in the Southern Shan States. Although Reed's identification queried the genus, it appears from Reed's figures that the specimen should be included within *Cyclospira*. Ventral and dorsal valves from rocks corresponding to the Naungkangyi Group at Taunggyi, Southern Shan States, figured by Reed (1932) as *Hyattidina* sp., might also be included here.

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APPENDIX

Rong *et al.* (1995) compared various affinity indices and found most useful those by Otsuka [$AI=C/(N_1N_2)^{1/2}$], Dice [$AI=2C/(N_1+N_2)$] and Fager [$AI=C/(N_1N_2)^{1/2}-1/(2(N_2)^{1/2})$]. In each formula N_1 is the total number of genera of one fauna, N_2 is the number of genera of another fauna and C is the number of genera common to both faunas, supposing N_2 is larger than N_1 . We have calculated the affinity indices between the eight faunas by all three methods and Table 1 shows each index in the lower diagonal and their average in the upper diagonal. Below are the lists of faunas used in the calculation of affinity indices:

1. Shihtzupu Formation (early Caradoc), northwestern Guizhou, South China (Xu *et al.* 1974, with some additional material collected by R. P. Tripp in the Natural History Museum, London): *Philhedrella* sp.; *Lingulella* sp.; *Nicolella actoniae*; *N. delicata*; *Saurorthis minor*; *Skenidioides* sp.; *Peritritoechia imbricata*; *Gonambonites nobilis*; *Leptellina sinensis*; *Aegironetes minuta*; *Anoptambonites* sp.; *Chonetoida* sp.; *Leptaena qianbeiensis*; *Platymena?* *mutabilis*; *Bellimurina rudis*; *Rafinesquina?* sp.; *Kiaeromena* sp.; *Glyptomena* sp.; *Syntrophopsis* sp.; *Porambonites triquetrus*; *P. transversus*.
2. Pingliang Formation (late Caradoc), Longxian, Shaanxi Province, Northwest China (Fu 1982, Rong & Zhan 1996): *Paracraniops* sp.; *Dolerorthis* sp.; *Bicuspina regularis*; *Glyptorthis* sp.; *Skenidioides* sp.; *Anisopleurella* sp.; *Leptestiina longxianensis*; *Leangella* (*Leangella*) sp.; *Sowerbyella* cf. *sladensis*; *Leptaena* sp.; *Gunnarella gigantea*; *Bellimurina quadrata*; *Kiaeromena longxianensis*; *Foliomena inelegans*; *Christiania longxianensis*; *Nubialba* sp.; indet. pentameroid; *Longxianirhynchia transversa*; *Cyclospira* sp.
3. Sargaldak Formation and its contemporary Anderken Formation (middle to late Caradoc), Chingiz, Kazakhstan (Klenina *et al.* 1984): *Ectenoglossa sorbulakensis*; *Tuvina extrema*; *Archaeorthis opima*; *Productorthis* sp.; *Austinella grandis*; *Perimeco-coelia semicostata*; *Aulie convexa*; *Sowerbyella rukavischnikovae*; *Ptychoglyptus* sp.; *Dulankarella* aff. *magna*; *D. namasensis*; *D. subquadrata*; *Craspedelia* sp.; *Leptaena* (*Leptaena*) *tarbagataiensis*; *Eoanastrophia extenuata*; *Camerella plicata*; *Rhynchotrema perspica*.
4. Khankhar Horizon (Caradoc), Gorny Altai, Russia (Kulkov & Severgina 1989): *Orthambonites jaboganicum*; *Altaeorthis uscutchevi*; *Hesperorthis concava*; *Boreadorthis togaensis*; *Glyptorthis altaica*; *G. balclatchiensis*; *Eridorthis subinexpecta*; *Multicostella* (*Chaulistomella*) *inaequistriata*; *M. (C.) amzassensis*; *Plectorthis apertus*; *P. altaicus*; *Plectorthis* sp.; *Mimella* sp.; *Severginella altaica*; *Paurorthis sibirica*; *Onniella chancharica*; *Triplesia mongolica*; *Palaeostrophomena* sp.; *Sowerbyites* cf. *lamellosus*; *Titanambonites elandicus*; *Iso-phragma ricevillense*; *Leangella scissa*; *Sowerbyella* (*Sowerbyella*) *sibirica*; *Bimuria bugrychiensis*; *Dactylogonia subgeniculata*; *Eoanastrophia lebediensis*; *E. aff. kurdaica*; *Togaella grandis*; *Rhynchotrema aincus*; *Rostricellula lapworthi*; *R. ainsliei amzassica*; *R. exilis*.
5. Nant Hir Group and Derfel Limestone (Caradoc), Bala District, Wales (Williams 1963): *Lingulella* cf. *ovata*; *Pseudocrania* cf. *divaricata*; *Paracraniops macella*; *Orbiculoidea* sp.; *Orthambonites cessata*; *Nicolella actoniae*; *N. actoniae obesa*; *Dolerorthis duftonensis proluxa*; *Dolerorthis* sp.; *Dinorthis flabellulum*; *D. berwynensis*; *D. berwynensis angusta*; *Platystrophia* cf. *sublimis*; *Rhactorthis crassa*; *Skenidioides* cf. *costatus*; *Cremnorthis parva*; *Dalmanella modica*; *Howellites striata*; *H. intermedia*; *H. ultima*; *H. antiquior*; *Onniella ostentata*; *O. cf. soudleyensis*; *Bancroftina* sp.; *Reuschella* cf. *horderleyensis*; *R. horderleyensis undulata*; *Heterorthis alternata*; *H. cf. retrorsistria*; *Salopia* sp.; *Bicuspina spiriferoides*; *Oxoplecia* sp.; *Vellamo* sp.; *Leptestiina oepiki*; *Sowerbyella sericea*; *S. soudleyensis*; *S. musculosa*; *S. sericea permixta*; *Eoplectodonta* cf. *rhombica*; *Sericoidea* sp.; *Strophomena grandis*; *Strophomena* sp.; *Glyptomena* cf. *osloensis*; *Macrocoelia expansa*; *M. prolata*; *Hedstroemia?* spp.; *Leptaena salopiensis*; *L. ventricosa*; *Kiaeromena* cf. *kjerulfi*; *Bellimurina incommoda*; *Rostricellula sparsa*; *Cyclospira* sp.
6. Cliefden Caves Limestone Group and equivalents (Caradoc), central New South Wales, Australia (Percival 1991): *Hesperorthis barbata*; *Ptychopleurella decretoria*; *Eridorthis australis*; *Dinorthis hadra*; *Bowanorthis fragilis*; *Plectorthis cliefdenensis*; *Doleroides mixticus*; *Phaceloorthis decoris*; *Boonderella fasciculata*; *Skenidioides quondonensis*; *Paraonychoplecia inversa*; *Sowerbyites isotes*; *Wiradjuriella halis*; *Anoptambonites exedra*; *Tylambonites speciosa*; *Sowerbyella billabongensis*; *Oepikina?* *walliensis*; *Trigrammaria ampla*; *Quondongia alitis*; *Molongcola variabilis*; *Christiania skolia*; *Didymelasma inconspicua*; *Rhynchotrema oepiki*; *Protozyga definitiva*; *Webbyspira principalis*; *Zygospira carinata*; *Australispira disticha*.
7. Advance Formation (Caradoc), northern Rocky Mountains, British Columbia, Canada (Jin & Norford 1996): *Plaesiomys* aff. *subquadratus*; *P. meedi*; *Dinorthis* cf. *holdeni*; *Glyptorthis assimilis*; *Scaphorthis perplexa*; *Platystrophia colbiensis*; *Paurorthis ponderosa*; *Paucicrura rogata*; *Oxoplecia globularis*; *Glyptambonites musculosus*; *Leangella* (*Leangella*) *biseptata*; *Christiania subquadrata*; *Bimuria* cf. *superba*; *Thaerodonta redstonensis*; *Eoplectodonta* (*Eoplectodonta*) *alternata*; *Strophomena* cf. *planumbona*; *Rafinesquina praecursor*; *Murinella* cf. *biconvexa*; *Oepikina* sp.; *Parastrophina* sp.; *Hiscobeccus mackenziensis*; *Anazyga bellicostata*.

A review of the stratigraphy and trilobite faunas from the Cambrian Burj Formation in Jordan

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SYNOPSIS. The Burj Formation in Jordan, and its correlatives in surrounding countries, is a Cambrian marine carbonate and siliciclastic deposit which transgressed widely but relatively briefly southwards across the Arabian craton. Three members (Tayan Siltstone, Numayri Dolomite and Hanneh Siltstone) are here formally described from outcrops at the southern end of the Dead Sea, Jordan. Trilobites from the Burj Formation are described and are all considered to be earliest Middle Cambrian in age, rather than Lower Cambrian, as previously recorded.

INTRODUCTION

The lithostratigraphy of the Cambrian System in Jordan has been studied extensively (Bender 1974; Powell 1989). In outline, Neoproterozoic complexes (Ibrahim & McCourt 1995) are overlain by the Ram Group, which consists dominantly of sandstone units and includes a fossiliferous carbonate-rich intercalation now known as the Burj Formation. Faunas from the Burj were examined by various workers who tentatively assigned early to mid- or late Cambrian and Ordovician ages to them. Contemporaneous beds which crop out at Timna in the southern Negev (south Israel) have been reviewed by Weissbrod (1970) and Parnes (1971); the Timna outcrop is generally accepted as being offset from the Dead Sea outcrop in Jordan by a left-lateral (sinistral) displacement of approximately 105 km along the Dead Sea – Gulf of Aqaba Rift fault (Freund *et al.*, 1970).

Brachiopods and trilobites recorded from the Burj Formation by Blanckenhorn (1912, 1914) were described by Richter & Richter (1941), who reviewed other work in that region. They rejected earlier opinions that the faunas ranged in age from early in the Cambrian to Ordovician, and regarded the records known to them as close to the Lower-Middle Cambrian boundary, and probably highest Lower Cambrian. Parnes (1971) described further material, especially from the southern Negev, and reviewed earlier work. After comparing material from the east side of the Dead Sea and from Timna in the southern Negev with Hupé's faunal succession for Morocco (Hupé 1960), he proposed a more elaborate biostratigraphy extending through much of the Lower Cambrian. Cooper (1976) studied the brachiopod faunas and relied on Parnes' work to indicate their late Early Cambrian age.

Subsequent seismic studies and the examination of deep boreholes has greatly extended knowledge of the Cambrian succession in Jordan (Andrews 1991). Although the macrofossils were considered to indicate a late Early Cambrian age for the formation, marine palynomorphs described from boreholes NH-1, TS-11, WS-3 in Jordan (Fig. 2), occurring in palynozone JC-1 of Keegan *et al.* (1990), were assigned an early Middle Cambrian age, especially on account of the occurrence of acritarchs known from the Oville Formation in Spain, which is assigned to the Leonian Stage (Table 1) and the overlying Caesaraugustian Stage (Liñán *et al.* 1993).

Whilst these reports suggested that the biostratigraphy of the Cambrian rocks of Jordan and Israel is complex, sedimentological syntheses, coupled with work on trace fossils, supported a relatively simple model in which a Cambrian marine transgression introduced a tongue of marine strata onto the Arabian craton (Selley 1972; Amireh *et al.* 1994), though those authors did not attempt to integrate their syntheses with the known biostratigraphy.

We have examined new material from the Dead Sea area and reviewed older work, especially in the light of recent study of the Moroccan sequences (Geyer 1990a, 1990b; Sdzuy 1995), and believe that the palaeontological evidence can be reconciled with the recent stratigraphical and sedimentological syntheses. We conclude (following Amireh *et al.* 1994) that near the beginning of Middle Cambrian times a marine incursion transgressed from the north or north-west onto earlier Cambrian fluvial deposits on the Arabian craton. It introduced various lithofacies comprising locally fossiliferous shallow-water carbonate and siliciclastic deposits. Soon afterwards a fall in sea-level and increased sediment from the Arabian craton resulted in a return to fluvial sedimentation which continued in central-south Jordan until the Ordovician.

LITHOSTRATIGRAPHY

LOCALITIES. Owing to a lack of a standard transliteration of Arabic place names, confusion has arisen regarding the names of wadis and other features referred to by various authors (for example Wadi Qunai has been recorded as Wadi Quni, Wadi Kneye, Wadi Gineya). We adopt the standard names used by the Geology Directorate, Natural Resources Authority, Jordan.

Localities studied during this work are located to within 500 m using the Palestine National Grid (PNG). Localities referred to by previous authors are not always precise, and here we have endeavoured to give a grid reference based on their descriptions.

Burj Formation

The Burj Dolomite-Shale Formation, hereafter referred to as the Burj Formation, forms a prominent cliff-like feature between the siliciclastic Salib Arkose and Umm Ishrin formations in the type

AGE		JORDAN (after Lloyd, 1969; Selley, 1970; Powell, 1988; Masri, 1988)		TIMNA (ISRAEL) (Weissbrod, 1970)		
SILURIAN LLANDOVERY	G R O U P	KUSHSHA SANDSTONE FM				
		MUDAWWARA SANDSTONE FM.	Ratiya Sst. Mbr			
			Batra Mst Mbr			
		DUBEIDIB SANDSTONE FM.	Tubeliyat Sst. Mbr.			
'upper'						
'middle'						
K H R E I M	G R O U P	HISWAH SANDSTONE FM.				
		UMM SAHM SANDSTONE FM				
		DISI SANDSTONE FM				
O R D O V I C I A N	G R O U P	UMM ISHRIN SANDSTONE FM.		NETAFIM FM SHEHORET FM		
		BURJ FM.	Hanneh Siltstone	Kushelba Sst.	TIMNA FM.	Mikhrot Mbr. Nehushtan Mbr. Nimra Mbr.
			Numayri Dolomite	Tayan Siltstone		Hakhlil Mbr
C A M B R I A N	R A M	SALIB ARKOSE FM		AMUDEI SHELOMO FM		
		FEINAN GRANITE & AHEIMIR VOLCANICS		ZENEFIM/EILAT FM		
		HIYALA VOLCANICLASTICS SARAMUJ CONGLOMERATE				
A Q A B A C O M P L E X		PRE-CAMBRIAN BASEMENT				

Fig. 1 Stratigraphical framework of the Cambrian and Ordovician rocks in Jordan and Israel (after Powell, 1989).

Bender (1974) termed it the 'dolomite-limestone-shale formation' and followed the definition of Blanckenhorn (*op. cit.*). However, in lithological sections and maps Bender (1968) included about 30 metres of overlying shales and sandstone (cb 2+1) within the same formation. The latter definition was adopted by Powell (1988) and is followed here, although in the subsurface Andrews (1991) placed the top of the formation at the top of the Numayri Dolomite. Powell recognised three members, in upwards sequence: the Tayan Siltstone, Numayri Dolomite and Hanneh Siltstone, described below, from the type area near Safi (Figs 3–5).

The Burj Formation is equivalent to the Timna Formation (Fig. 1) on the west side of the Wadi Araba, at Timna, near Eilat (Weissbrod, 1970). The four formations of Parnes' (1971) review – the Hakhlil, Nimra, Nehushtan and Mikhrot formations – are here treated as members of the Timna Formation.

Tayan Siltstone Member. This ranges in thickness from 18–20m, and consists of finely laminated green, mauve and red or buff, micaceous, fine-grained sandstone and siltstone.

The name is taken from Wadi Tayan (PNG 201.5:061.5) where the member is well exposed (Figs 3, 5). Straight-crested, oscillation (wave) ripples, ripple cross-lamination, and parallel lamination are common. The thicker sandstone beds have small-scale, bimodal, trough cross-bedding with mudstone intraclasts. Thin dolomite

lenses are present near the middle of the member, and indeterminate surface burrows are common on some bedding planes. Secondary gypsum veins and laminae occur along joints and bedding planes. The lower boundary is defined at the base of mauve-red micaceous siltstone and fine-grained sandstone that overlies yellow-brown medium-grained trough cross-bedded sandstone of the Salib Arkose Formation. The upper junction with the Numayri Dolomite is taken at the base of the first thick bed of limestone or dolomitic limestone, which in places is sandy, with low-angle erosive scours and ripple cross-lamination.

Numayri Dolomite Member. The member (38 to 60 m thick) forms a prominent, brown-weathering cliff along the outcrop. The name derives from Wadi Numayri (PNG 203:059) where it is well exposed. The carbonate varies from limestone to dolomitic limestone and dolomite with wackestone and packstone textures; clasts include oolites and bioclasts (brachiopods, hyolithids and trilobites). The vertical sequence of microfacies varies throughout the outcrop, but the following generalised sequence is common to most exposures in the Safi – Wadi Numayri areas: the basal 5 m has a high proportion of fine-grained quartz sand with ripple cross-lamination and sandstone intraclasts; this passes up to a massive, brown-weathering (grey) dolomite and dolomitic limestones (microcrystalline, wackestone and packstone textures), 20–30 m thick, with glauconite peloids, cross-laminated and parallel-laminated oolites, oncolites (algal-coated grains), and lenses of disarticulated brachiopods and rare trilobite fragments. Irregular lenses of orange-brown dolomite are intercalated with the clast-rich carbonates. There is an increase in quartz sand above, with alternating sand-rich and sand-poor lenses; the sand-rich lenses are cross-laminated, with shallow erosive scours and they weather as prominent dark brown chert-like bands, 2–3 m thick. Beds of oolitic, oncolitic or brachiopod shell-rich dolomitic limestone are locally present at the top of the member in the south. Near Safi (Figs 4, 5), the member is thicker (58 m) and the upper part includes beds of cross-laminated oolitic limestone, algal stromatolites, and thin (40 cm) beds of green calcareous siltstone with abundant trilobite fragments, hyolithids and glauconite peloids. Here, the sequence is capped by a distinctive orange-weathering dolomite. The textures and fine details of the carbonates are often obscured at outcrop by ubiquitous brown staining. The boundary with the green, red or grey micaceous siltstone or fine-grained sandstone of the overlying Hanneh Siltstone is sharp.

Hanneh Siltstone Member. The name is taken from Jibal Tabaq Hanneh (PNG 201.5:060.0), on the north side of Wadi Numayri (Fig. 3). The lithology of this member is similar to the Tayan Siltstone, but there is a higher proportion of sand over silt-grade siliciclastic rocks. It was not previously included in the formation, except for the maps and lithological sections in Bender (1968). It is about 30 m thick in the Wadi Saramuj area and 35 m thick in the cliffs below Jibal Tayan. The base is sharp, and is taken where red-grey or green parallel-laminated to ripple cross-laminated micaceous siltstone overlies the carbonate (Numayri Dolomite). The beds above are laterally variable, but predominantly comprise thinly bedded green or red-green, micaceous, ripple cross-laminated siltstone and micaceous fine-grained sandstone, with thicker beds (0.5 m) of buff, medium-grained, bimodal trough cross-bedded sandstone; mudstone and dolomite clasts are common at some horizons. Small, circular surface-burrows and *Rusophycus*(?) traces are present on siltstone surfaces. The top is clearly marked by the overlying red-brown, massive, medium- to coarse-grained, large-scale trough cross-bedded sandstone (Umm Ishrin Formation).

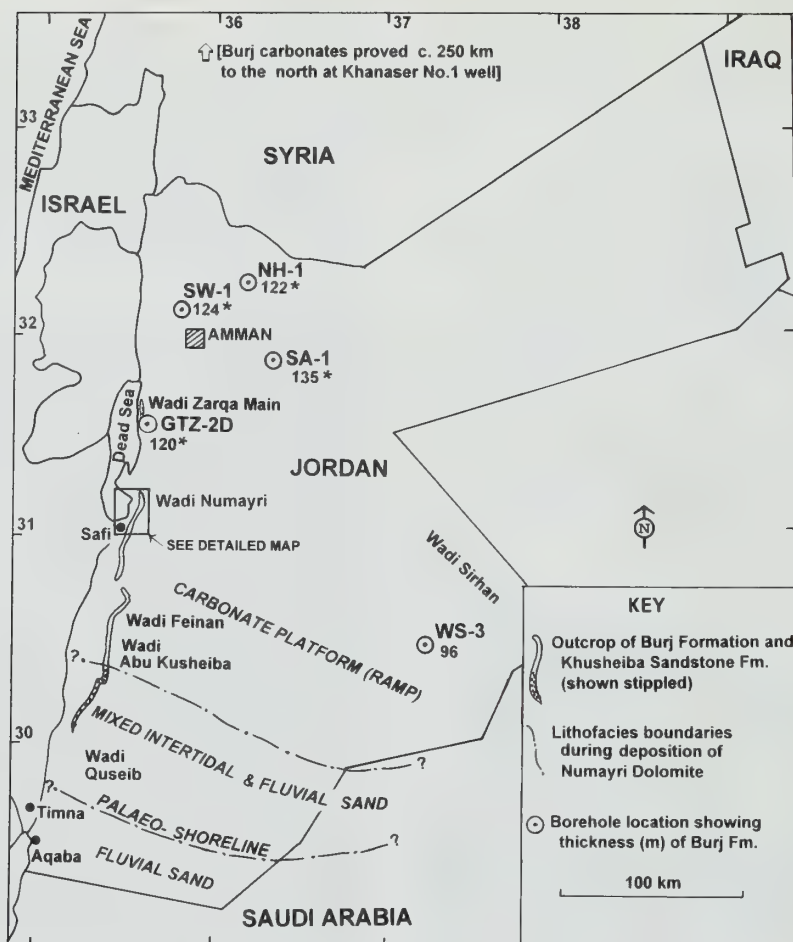


Fig. 2 Sketch-map showing the outcrop of the Burj Formation in Jordan and the position of localities mentioned in the text. Lithofacies boundaries obtaining during deposition of the Numayri Dolomite are shown for southern Jordan. Degrees of latitude and longitude are shown at the edge of the map. Selected boreholes: GTZ-2D = Geothermal Zarqa Main-2D, NH-1 = Northern Highland 1, SA-1 = Safra 1, SW-1 = Suweileh 1, WS-3 = Wadi Sirhan 3. An asterisk indicates the minimum thickness of the Burj Formation in boreholes where the Hanneh Siltstone was not recognised and the top of the formation was taken at the top of the Numayri Dolomite Member (*sensu* Andrews, 1991).

Zarqa Ma'in outcrop. The outcrop 1 km north of Wadi Zarqa Ma'in (Fig. 2) is incomplete as only the upper part of the formation is exposed (Fig. 6). The succession probably belongs to the uppermost part of the Numayri Dolomite Member and/or the Hanneh Siltstone Member. At this locality about 3 m of grey finely laminated, fine-grained quartz arenite with burrows and ripple cross-lamination, at the base, are overlain by intercalated green-grey, cross-laminated siltstone, fine-grained sandstone and shelly grainstone, passing up to oolitic packstone and cross-bedded trilobite grainstone (4 m). The eroded top of the latter is overlain by marine siliciclastic rocks with bimodal cross-bedding, trilobite traces and *Harlania* burrows (24.5 m). A second carbonate unit (3 m) follows above, consisting of trilobite, brachiopod, hyolithid grainstones, oolitic and cross-bedded in part, and this in turn is overlain by about 50 m of marine siliciclastic strata. These consist of fine- to medium-grained bimodal trough cross-bedded sandstones with small dune forms, intercalated with parallel laminated, ripple cross-laminated, green to mauve, micaceous siltstone and fine-grained sandstone with oscillation and interference ripples. Sparse surface traces and burrows are present in the fine-grained lithologies.

ENVIRONMENT OF DEPOSITION

Early workers (Hull 1886; Blanckenhorn 1914) recognised the marine nature of the formation by the presence of brachiopods, trilobites and hyoliths in the carbonates; subsequently, marine calcareous algae, including *Girvanella* sp., were identified by J. H. Powell in thin sections of the oncolite lithofacies. The siliciclastic strata contain an ichnofauna characteristic of shallow-water environments, including the arthropod resting and crawling traces *Rusophycus* and *Cruziana*, which are common on some of the bedding planes in the Tayan Siltstone and Hanneh Siltstone members, and sub-vertical burrows, including *Skolithos*. Amireh *et al.* (1994) also identified *Diplocraterion* and *Tigillites* from the Hanneh Siltstone at Wadi Numayri, and *Cruziana aegyptica* Seilacher (1990), *Diplocraterion* sp. and *Scolecia* sp. from siliciclastic rocks at Wadi Quseib.

From the base upwards, a clear pattern of marine transgression and regression is indicated by the fauna and sedimentary structures in the Wadi Numayri type area (Powell 1988, 1989; Amireh *et al.*, 1994). The Tayan Siltstone overlies medium-grained sandstones

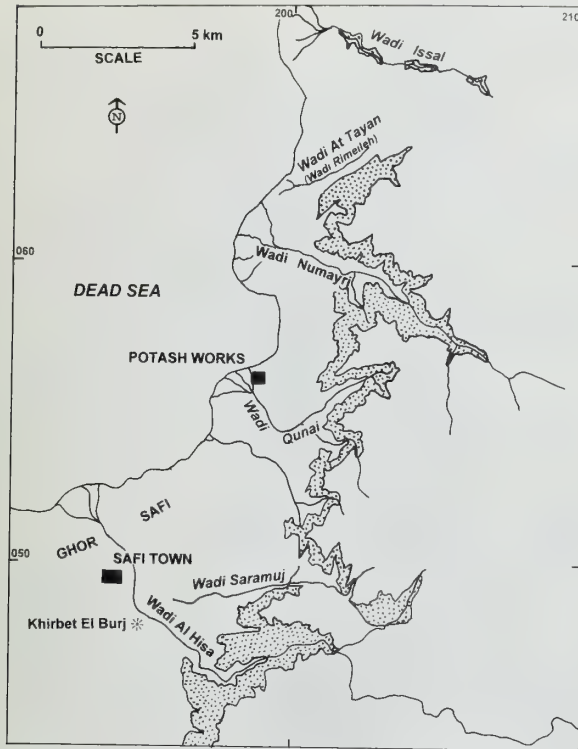


Fig. 3 Generalised map of the Safi area, southern Dead Sea, showing the outcrop of the Burj Formation (stippled), and the localities mentioned in the text. The grid is Palestine National Grid (PNG); geological boundaries after Powell (1988).

with laterally accreted channel-fill, probably of meandering-river or tidal-flat origin. Wave ripples, small-scale bidirectional cross-bedding, intra-clasts, burrows and thin dolomite laminae in the Tayan Siltstone suggest a marine incursion over a low-lying alluvial plain, and deposition in a shallow subtidal to intertidal environment. The succeeding carbonates (Numayri Dolomite) mark the maximum phase of the transgression. Oncolites, oolites, disarticulated brachiopod shell lenses, low-angle cross-bedding with shallow scours in the purer carbonates, and ripple cross-lamination in the siliciclastic-rich carbonates indicate deposition in a warm, shallow, carbonate lagoon, with periodic storm-events redistributing oolites, bioclasts and quartz sand. Domal, laterally linked stromatolites indicate intertidal to supratidal conditions near the top of the unit. The Hanneh Siltstone represents the regressive phase marked by an influx of siliciclastic sediment, derived from the south, into the shallow carbonate platform. Sedimentary structures and trace fossils similar to these in the Tayan Member suggest deposition in a tidally dominated shoreline. Subsequently, coarse-grained, trough cross-bedded sand was deposited, by braided to meandering rivers, which prograded over the wedge of marine sediments. In central and south Jordan, continental fluvial deposition continued through the Umm Ishrin Formation into the Disi Formation (Selley 1972). Trace fossils in thin marine intercalations suggest that the Disi Formation is of early Ordovician age (Seilacher 1970).

At Wadi Zarqa Ma'in the exposed carbonates show an upward-coarsening (shoaling) trend from shallow-water ripple cross-laminated siltstones and sandy carbonates to oolitic shelly packstones and cross-bedded (trilobite-rich) grainstone deposited in the shallow subtidal zone. Bi-directional dune sandstones with an erosive base, and bioturbated ripple cross-laminated siltstones above, suggest an influx of sand from prograding rivers along the shallow, tidally influenced coastal margin. The upper carbonate bed marks a brief transgressive pulse and was deposited in a shallow subtidal to

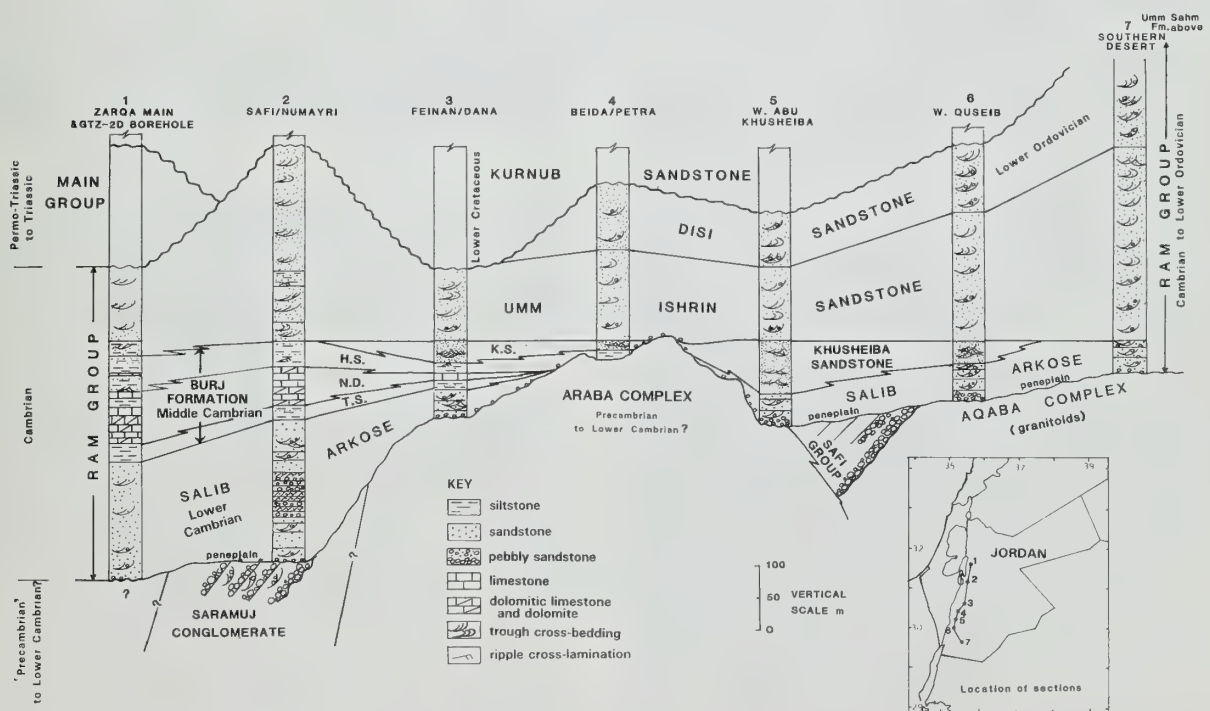


Fig. 4 Correlation of the Ram Group, including the Burj Formation, along the margin of the Dead Sea - Gulf of Aqaba Rift. Inset map shows the location of the sections. HS = Hanneh Siltstone, KS = Kusheiba Sandstone, ND = Numayri Dolomite, TS = Tayan Siltstone (after Powell, 1989).

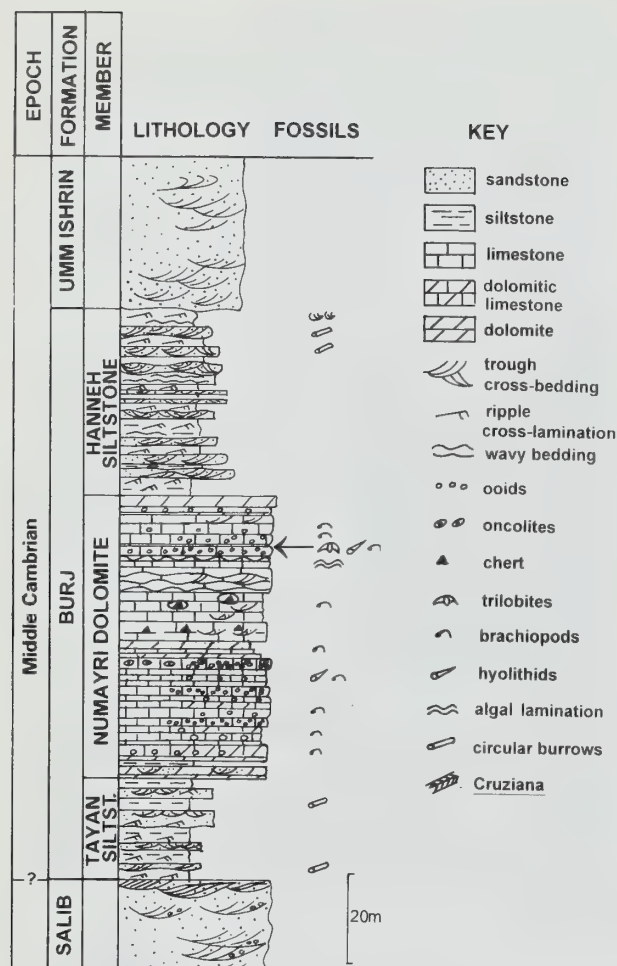


Fig. 5 Composite lithological section of the Burj Formation in the Safi area, southern Dead Sea. Arrow shows the level with trilobites in Wadi Qunai (after Powell, 1989).

intertidal environment; it was succeeded by a further pulse of tidally influenced shallow-marine siliciclastic deposition under similar conditions to those of the Tayan Siltstone further south.

The pattern of southwest- to west-trending facies belts derived from deep boreholes (Andrews 1991), passing from fluvial and intertidal siliciclastic facies in south Jordan to shallow marine carbonate and intertidal siliciclastic environments in central and north Jordan, is consistent with a progressive onlap during Tayan to Numayri time. The carbonate platform can be traced in the sub-surface of north Syria (Best *et al.* 1993), a distance of about 700 km from the location of the palaeoshoreline in south Jordan (Fig. 2). The maximum transgression (maximum flooding) resulted in deposition of the main Numayri carbonate in the type area, passing southwards into intertidal and fluvial siliciclastic strata (Wadi Kusheiba Sandstone). A subsequent regressive low-stand of sea-level (see Regional Correlation, below) resulted in an increased influx of sandy sediment during deposition of the Hanneh unit in the type area. However, boreholes in north Jordan indicate that stratigraphically younger phases of carbonate deposition may have continued in those areas located farther offshore.

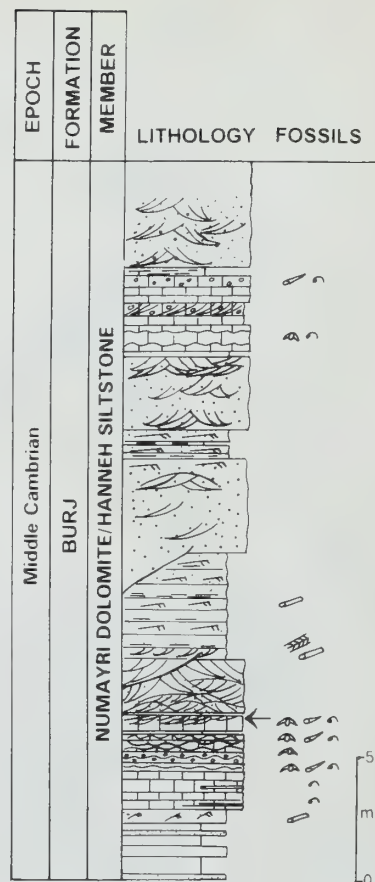


Fig. 6 Stratigraphical section of the upper part of the Burj Formation at Wadi Zarqa Ma'in, northern Dead Sea. Key as for Fig. 5, but note the difference in the vertical scales. Arrow shows the level with the trilobites figured herein.

FAUNAS

Fossils are reported from the following sites:

1. WADI ZARQA MA'IN. A section 800 m north of Wadi Zarqa Ma'in (PNG 204.4:501.3) contains thin calcarenite beds. These have yielded:

'Hyolithes' kingi Richter & Richter, 1941 [type locality]
Kingaspis campbelli (King, 1923) [type locality; described herein]
Palaeolenus antiquus (Chernysheva, 1956) [described herein]

'Hyolithes' kingi is apparently identical to *Hyolithes fouchouensis moabiticus* described from the same locality by Picard (1942), presumably in ignorance of the Richter & Richter (1941) paper.

2. WADI RIMEILEH, King's (1923) locality λ3 (PNG 201:061), 1.6 km south of Wadi 'Esal' (=Issal); this is approximately the same locality as Wadi At Tayan (Fig. 3), described herein. From micaceous siltstone:

Onaraspis palmeri (Parnes, 1971)

It appears that the original material of *Realaspis? orientalis*

- (Picard, 1942) came from the same locality, though not necessarily the same stratum.
3. WADI QUNAI. Section 2 km east of Arab Potash Works, Safi (PNG 201.5:055.6) (Fig. 3):
Lingulate? brachiopod with divaricate sculpture
'Hyolithes' cf. *kingi* (Richter & Richter, 1941)
Realaspis sp. nov. [described herein]
Redlichops blanchenhorni Richter & Richter, 1941 [described herein]
 4. WADI SARAMUJ (PNG 198:047) (Fig. 3):
Psiloria alata (King, 1923) [type locality]
Trematosia radifer (Richter & Richter, 1941) [type locality]
'Hyolithes' sp.
 The brachiopods were described by Cooper (1976).
 5. KHIRBET EL-BURJ (PNG 198:047) (Fig. 3):
Trematobolus palastinensis Richter & Richter, 1941 [type locality]
Trematosia radifer (Richter & Richter, 1941)
'Hyolithes' sp.
Hesa problematica Richter & Richter, 1941 [type locality]
Redlichops blanchenhorni Richter & Richter, 1941 [type locality; described herein]
 6. AL ABRASH, Ghor-es-Safi; exact locality and PNG reference not known.
Psiloria dayi Cooper, 1976 [type locality]
Trematosia radifer (Richter & Richter, 1941)
Kingaspidoidea cf. *obliquoculatus* Geyer, 1990b [described herein]

Farther south, from the Timna area in Israel, Parnes (1971) described several trilobites, namely species of *Strenuella* and the new genus *Timnaella*, together with '*Myopsolenus*' *palmeri* Parnes for which the type locality is Har 'Amram, south of Timna. The material is fragmentary and poorly preserved, and correlation is uncertain, but we have confirmed Parnes' (1971: 204) suggested identification of King's 'asaphid' from Wadi Rimeileh with his *Onaraspis* [*Myopsolenus*] *palmeri*, which we take to be of about the same age as the beds at Wadi Qunai. Cooper (1976) described nine brachiopods from the Timna area, none of which have yet been identified from around the Dead Sea.

REGIONAL CORRELATION

The problem of recognising the Early-Middle Cambrian boundary is discussed by Geyer & Palmer (1995). If the presence of *Paradoxides* s.l. is used to recognise the Middle Cambrian, the appearance of *Acadoparadoxides* in Morocco at a level considerably lower than that indicated by earlier workers (e.g. Hupé 1960) implies that previous records of Lower Cambrian faunas may now need to be re-classified as Middle Cambrian – an opinion already expressed by Öpik (1975). The interval affected approximates to the lower Amgan (Table 1) of the Siberian succession and includes the *Protolenus* Zone of North Atlantic (Avalonian) successions. At present no internationally agreed standard has been adopted (Geyer & Palmer 1995: 462), but in the present paper the Moroccan usage of Geyer (1990a) and Geyer & Palmer (1995) is adopted to facilitate correlation in the Mediterranean area. In 1990 Geyer took the base of the Middle Cambrian at the base of the *Hupeolenus* Zone, although Geyer & Palmer (1995) showed *Paradoxides* s.l. extending down into its uppermost part only. In the following discussion reference is made to the stratigraphical successions shown in Table 1.

WADI ZARQA MA'IN. The two trilobites recorded from Wadi Zarqa Ma'in are known elsewhere. In Siberian sections on the rivers Amga and Lena *Palaeolenus antiquus* characterises the *antiquus* Zone, the basal zone of the Middle Cambrian as traditionally recognised there, and the range of *Schistocephalus juvenis* lies immediately above that of *P. antiquus*. In Morocco *S. cf. juvenis* occurs with *Acadoparadoxides* in the *Cephalopyge* Zone (Sdzuy 1995), and it is assumed that the *P. antiquus* Zone correlates with the underlying beds, i.e. approximately the *Hupeolenus* Zone. *Kingaspis campbelli* is recorded from Morocco (Geyer 1990b: 44) in strata questionably referred to the *frequens* Zone (Table 1), the third zone above the base of the Middle Cambrian as recognised by Geyer (1990a). Assuming that the more reliable evidence is the *Palaeolenus-Schistocephalus* sequence, the upper part of the Burj Formation at Wadi Zarqa Ma'in is correlated approximately with the *Hupeolenus* Zone.

SOUTHERN END OF DEAD SEA. It is more difficult to assess the age of the Burj Formation in the type area as nearly all the fossils are known only from the Dead Sea and Rift Valley region. *Kingaspidoidea* cf. *obliquoculatus* is closest to a species known from the *Hupeolenus* Zone in the lowest Middle Cambrian of Geyer's (1990a) Moroccan sequence. The metadoxidid *Realaspis*, which has a relatively distinctive pygidium, is known by the type and only described species *R. strenoides*; this genus, with *Pseudolenus*, characterises the base of the Bilbilian in Spain (Liñán *et al.* 1993), a level that has been correlated with the the lowest Middle Cambrian of Geyer, namely the *Hupeolenus* Zone. The fragments of *Onaraspis palmeri* (Parnes) from Wadi Rimeileh (= Wadi At Tayan) suggest probable correlation of the Burj Formation with the Mikrot and/or Upper Hakhilil members of the Timna Formation of the Timna area (Parnes 1971). All the other species described from that region appear to be endemic and the genera they represent are either new or stratigraphically long-ranging (Parnes 1971; Cooper 1976).

DISCUSSION. The stratigraphical resolution of these faunas for wider correlation is not very good, but, so far as can be judged, they all indicate a comparatively restricted stratigraphical level close to the Lower-Middle Cambrian boundary as recognised by Geyer (1990a) and Geyer & Palmer (1995). They indicate correlation of the Burj Formation with the *Hupeolenus* Zone of Morocco, probably with the lower part of the Bilbilian Stage of Spain, and with the lowest part of the Amgan Stage in Siberia. Sdzuy (1995) demonstrated the correlation of overlying strata: the *Cephalopyge* Zone of Morocco with the lowest Leonian of Spain and the middle zone of the Amgan (Table 1).

According to Liñán & Gámez-Vintaned (1993: 838), strata in Spain show evidence of what they term the Daroca Marine Regression during the Bilbilian Stage at a level somewhat above its base, and they attribute it to a eustatic fall of sea-level. If our correlation of the Burj Formation with the lower Bilbilian is correct, it is probable that it was the Daroca Regression which re-established fluvial deposition over Jordan and on the Arabian Craton. The sea retreated towards Turkey where, although correlatives of the *Hupeolenus* Zone have not been recorded, faunas of Middle Cambrian age are well described by Dean and his co-workers (e.g. Dean & Özgül 1994): such faunas commence with approximate correlatives of the *Cephalopyge* Zone, and range up through the Middle Cambrian, and confirm the persistence of marine deposition in areas to the north of Jordan and Syria.

SYSTEMATIC DESCRIPTIONS

Superfamily **REDLICHIOIDEA** Poulsen, 1927

Family **REDLICHIIDAE** Poulsen, 1927

?Subfamily **PARAREDLICHIIINAE** Hupé, 1953

Genus **REDLICHOPS** Richter & Richter, 1941

TYPE SPECIES. *Redlichia (Redlichops) blanckenhorni* Richter & Richter, 1941, by original designation.

DISCUSSION. *Redlichops* is a poorly known genus. When Chang [=Zhang] (1966) and Zhang *et al.* (1980: 79) reviewed redlichiid trilobites they referred *Redlichops* with doubt to the Pararedlichiinae, mainly because both the anterior and posterior ends of the palpebral lobe are set rather far from the glabella. Even so, *Redlichops* differs from other Pararedlichiinae in the great width of the interocular area of the fixigena and in the recurved palpebral lobe, features matched or exceeded only by the aberrant Metaredlichiine *Jingyangia* (Zhang

et al. 1980: pl. 31, figs 7, 10, 11). However, the glabella of *Redlichops* is not comparable with the parallel-sided or clavate glabella of the Metaredlichiinae, and the genus is here retained provisionally in the Pararedlichiinae, following Chang (*in* Whittington *et al.*, 1997: 440).

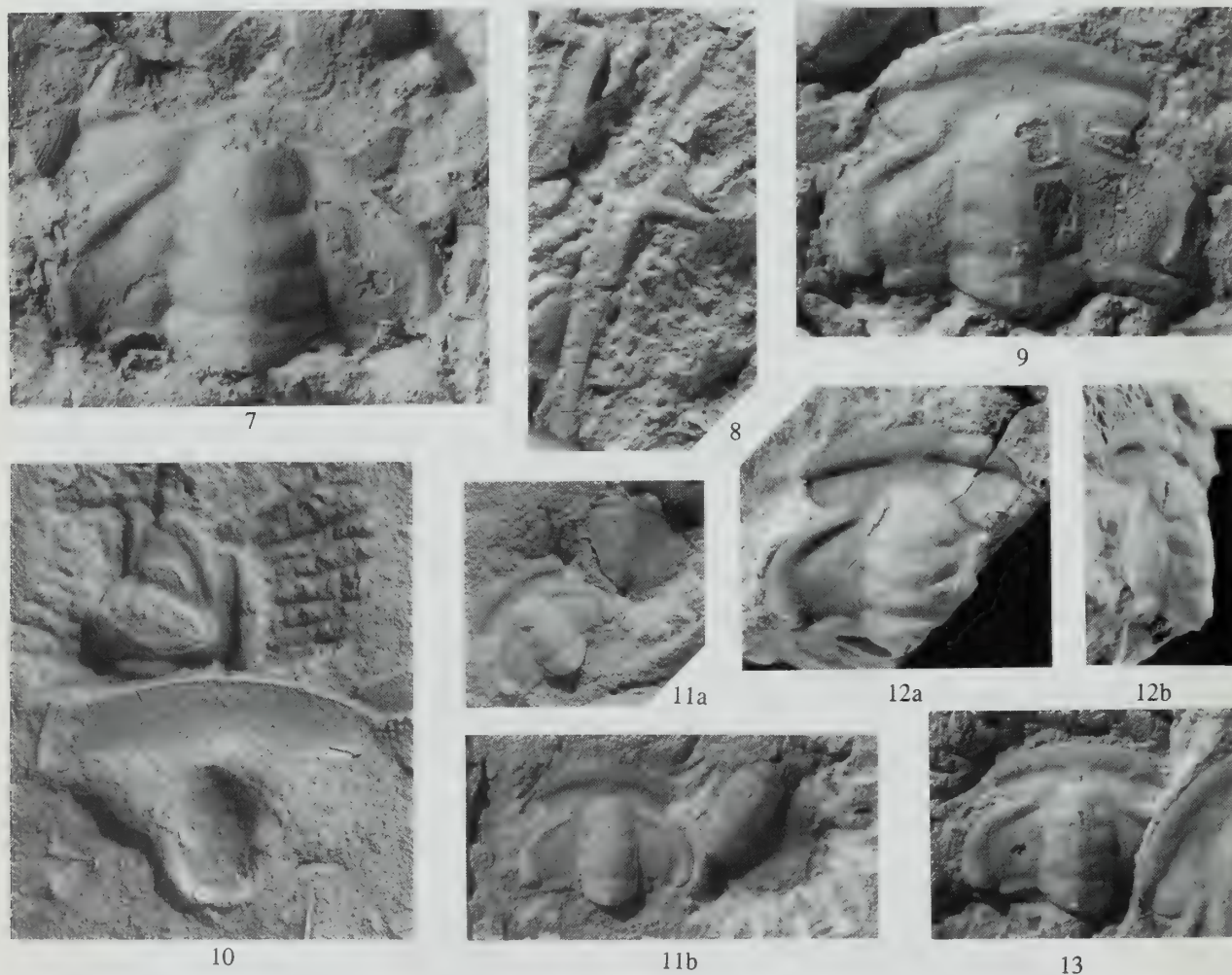
Redlichops blanckenhorni Richter & Richter, 1941

Figs 7–13

1941 *Redlichia (Redlichops) blanckenhorni* Richter & Richter: 15, pl. 2, figs 1, 2, 4, 5?, 6a (*non* figs 3, 6b) [synonymy, description].

1997 *Redlichops (R.) (sic) blanckenhorni* Richter & Richter; Whittington *et al.*: 441, fig. 280.1.

MATERIAL. The species is based on fragmentary material from the type locality, Khirbet el Burj. Dr W. Struve kindly made available plaster casts of the holotype (Senckenberg Museum, Frankfurt-am-Main X1287a; Fig. 7) and a paratype (X1287b). New material from Wadi Qunai referred to the species is somewhat weathered but is



Figs 7–13 *Redlichops blanckenhorni* Richter & Richter. 7, plaster cast (It.26207/1) of **holotype**, Senckenberg Museum X1287a, $\times 4$. Khirbet El-Burj. 8–13, Wadi Qunai, Safi. 8, librigena It.26211/5, $\times 4$. 9, large cranium, It.26209/1, $\times 4$. 10, external mould of rostral-hypostomal plate, associated with *Realaspis* sp. nov. (Fig. 16), It.26212/1, $\times 4$. 11a, b, small cranium It.26209/3, associated with fragmentary pygidium It.26209/4 attributed to the same species; 11a $\times 3.5$, 11b $\times 4$. 12a, b, top and side views of cranium, It.26209/6, $\times 4$. 13, cranium It.26209/2, $\times 4$.

more complete, and consists of nine cranidia and some cranidial fragments, a rostral-hypostomal plate, three librigenae, and a fragmentary pygidium tentatively referred to this species (BM It26209, It26211-3).

DESCRIPTION AND DISCUSSION. The new specimens show that, despite their fragmentary material, the Richters' description and reconstruction of the cranidium are generally correct. The preglabellar field is slightly longer than they showed it, and in small specimens is crossed by a preglabellar ridge or plectrum; the anterior border bears faint terrace-lines parallel to the margin. The palpebral lobes in the new material are more evenly curved than in the reconstruction by Richter & Richter (1941: pl. 2, fig. 6a); in the new material they do not show the distal narrowing described by Richter & Richter, nor is this very evident in their holotype (Fig. 7). The palpebral-ocular ridge is not joined anteriorly to the glabella, nor is a parafrontal band evident; this ridge appears to slope backwards more steeply in the holotype than in the similarly sized specimen in Fig. 9, but there is some variation in this feature among the various specimens on block It.26209 (Figs 9, 11–13). The postocular section of the facial suture is very short. Where unweathered the surface is seen to be finely granulose.

The rostral-hypostomal plate (Fig. 10) is abraded but resembles those of other Redlichidae (Zhang *et al.* 1980: 69). If correctly assigned to this species, it shows that *Redlichops* is conterminant. The presence of a plectrum crossing the preglabellar field is commonly seen in trilobites with conterminant hypostomes.

The librigena (Fig. 8), confidently assigned because the course of the facial suture corresponds to that of the cranidium, is narrow, the border and the field within the border being of about the same width; in this it differs from the large fragment figured by Richter & Richter (1941: pl. 2, fig. 3), which we exclude from the species.

One fragmentary pygidium (Figs 11a–b) has a long, poorly segmented axis and the pleural field nearly as wide as the axis. There is one weak pleural groove. The surface is finely granulose and has fine striae sub-parallel to the margin. The sculpture is much less conspicuous than that of the pygidia from the same beds assigned to *Realaspis*.

The broad interocular areas of the fixigenae and the recurved palpebral lobe make *Redlichops blanckenhorni* a distinctive taxon, and no closely similar species is known. At a comparable size the Pararedlichiine *Eoredlichia yaoyingensis* (Kobayashi) has narrower interocular fixigenae and shorter palpebral lobes, but immature forms have relatively longer, more curved palpebral lobes (Zhang *et al.* 1980: pl. 35, fig. 10), suggesting that the peculiarities of *Redlichops* may be progenetically derived.

HORIZON. *Redlichops blanckenhorni* is known only from Jordan and its biostratigraphical significance is not established. Pararedlichiinae occur typically in the low Lower Cambrian but are not known to range into the Tissaftin Stage which is low Middle Cambrian in Geyer's (1990a) usage. However, *Redlichops* is only doubtfully referred to the Pararedlichiinae, and is here considered to lie close to the Lower-Middle Cambrian boundary, as originally suggested by Richter & Richter (1941: 27).

Subfamily METADOXIDINAE Whitehouse, 1939

Genus *REALASPIS* Sdzuy, 1961

TYPE SPECIES. *Realaspis strenoides* Sdzuy, 1961, by original designation.

DISCUSSION. Sdzuy (1961) placed *Realaspis* in the Neoredlichi-

inae, and Chang (*in* Whittington *et al.*, 1997: 458) referred it to the subfamily Resseropinae, family Saukiandidae. However, the relatively broad interocular area of the fixigenae and the short palpebral lobe favour reference to the Metadoxidinae, as suggested by Öpik (1968: 151).

Realaspis sp. nov.

Figs 15–18

MATERIAL. Four incomplete cranidia, one librigena, two pygidia, and several doubtful granulose fragments, associated with *Redlichops blanckenhorni* at Wadi Qunai (BM It26210-2).

DESCRIPTION. Glabella tapered, rounded in front; glabellar furrows very weak, seen on the largest cranidium as faint indentations in the side of the glabella; occipital ring with small spine (Fig. 15a), occipital furrow weak. Anterior border strong, with striae sub-parallel to anterior margin. Preglabellar field practically absent, forming a depressed groove shorter than border. Palpebral-ocular ridge strong, oblique, not confluent with glabella, but in the smaller figured cranidium (Fig. 16) seems to extend into a parafrontal band. The eye extends approximately from the second glabellar furrow (S2) to the occipital furrow (SO). At level of anterior end of eye the width of cranidium is nearly three times the glabellar width at the same level; at the posterior end of the eye it is a little more than twice as wide. Interocular area of fixigena has a marked elongated interocular swelling (Pillola 1993: 859) close to the glabella. Preocular section of facial suture short, straight, subparallel or slightly divergent forwards to the anterior border furrow; posterior section very short. Surface with coarse but not very closely spaced granules. Several fragments on the same bedding planes (Fig. 17) bear the same sculpture and indicate the presence of much larger individuals than the figured specimens.

Two pygidia (Fig. 18) associated with *R. blanckenhorni* and *Realaspis* sp. nov. are referred to the latter because their granulation and coarsely striate margins resemble those of the cranidia assigned to *Realaspis*. Outline rounded, with length two-thirds of the width. The axis occupies less than half the width and nearly the whole length of the pygidium and has one distinct and one obscure axial ring. The pleural regions have one or two pairs of weak furrows and the margin is entire; there is no semi-ankylosed anterior segment. Surface granulose, with striae near to and subparallel with the margin.

DISCUSSION. The pygidia of the present taxon are fairly distinctive, most resembling those of the Neoredlichiinae and some Metadoxidinae, especially *Realaspis strenoides* Sdzuy (1961: pl. 4, figs 18–24), though it has 1–2 rather than 3 axial rings. The cranidium is also similar in outline to *R. strenoides* (Sdzuy 1961: 536 (254), pl. 4, figs 1–12), but shows more marked relief: in *R. strenoides* the anterior border and palpebral-ocular ridge are not so strong, the border furrow in front of the glabella is narrower, the eye is shorter, no interocular swellings are seen and there is no occipital spine (Whittington *et al.*, 1997: fig. 249.1a). The sculpture in *R. strenoides* is unknown, so the granulation of the present species and the striae on the anterior border cannot be compared.

The present cranidia resemble some bigotinids related to *Hupetina* Sdzuy, 1978, from the lowest trilobite zone in the Issendalen Stage of the Moroccan Cambrian (Geyer 1990a). They differ from *Hupetina antiqua* Sdzuy in having weaker glabellar furrows, a stronger anterior border and longer preglabellar field; the interocular swelling is larger and closer to the glabella than in Sdzuy's (1978: pl. 1, fig. 7) paratype. In proportions and the weak glabellar furrows the present material is more like the unnamed cranidium from the Lemdad section A2, figured by Sdzuy (1978: fig. 3, top left), though that form

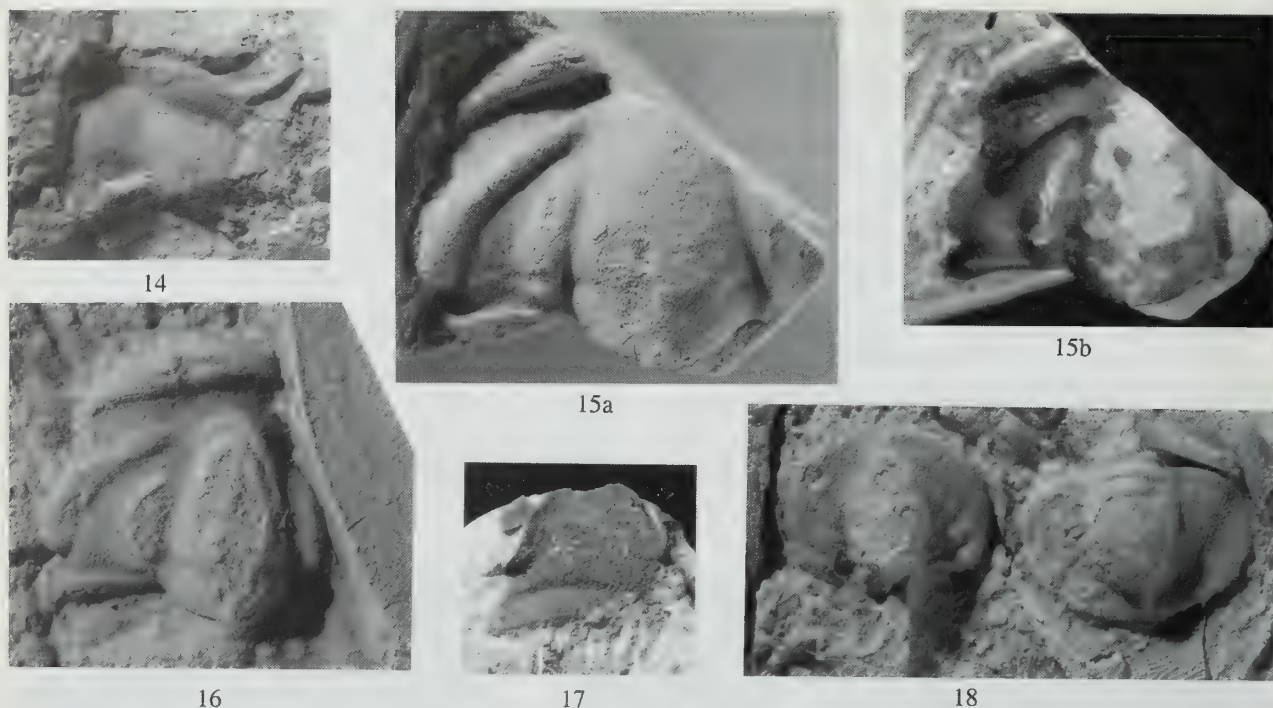


Fig. 14 *Hesa problematica* Richter & Richter, **holotype**; plaster cast (It.26207/2) of cranidial fragment, showing parts of the preocular suture and anterior border, Khirbet El-Burj, Senckenberg Museum X1287a, $\times 4$.

Figs 15–18 *Realaspis* sp. nov., Wadi Qunai, Safi. **15a, b**, abraded cranidium It.26210/1; 15a, whitened, shows the interocular swelling, occipital furrow and occipital node, $\times 3.5$; 15b, unwhitened, shows the course of the facial suture, $\times 3$. **16**, small cranidium It.26212/2, $\times 8$. **17**, fragment of fixigena of large cranidium attributed to this species, showing granulation, It.26209/8, $\times 3$. **18**, two pygidia, It.26211/1 (right) and 26211/2 (left), $\times 4$.

has more divergent preocular facial sutures and no interocular swelling is shown. Few bigotinid pygidia have been described, but those of the present species are unlike those of *Bigotina* itself (Pillola 1993: pl. 3, figs 3, 8).

The holotype of *Hesa problematica* Richter & Richter (1941: pl. 2, fig. 7) is a fragment of a large trilobite on the same block as the holotype of *Redlichops blanckenhorni*. It is unsuitable to be the formal representative of a distinct genus, but shows a slightly divergent preocular suture and a frontal border (Fig. 14) striated in much the same way as our Fig. 15; it differs because the glabella seems to indent the frontal border, a difference that seems too great to be attributed to the stage of growth.

Protolenus orientalis Picard (1942: 1, pl. 2, figs 1, 2) was revised by Parnes (1971: 186, pl. 1, figs 1–4), who figured two cranidia, including Picard's specimen. He referred the species to *Resserops* (*Richterops*) Hupé, 1953, though the form of the palpebral lobe is more compatible with *Realaspis*. Our material differs from *R. orientalis* in having a stronger, striated anterior border, a stronger border furrow, wider interocular fixigenae with stronger interocular swellings, and a coarser granulation. However, *Realaspis orientalis* seems to show greater resemblance to *Hesa problematica*, but the type material of the latter is so fragmentary that full comparison cannot be made.

HORIZON. *Realaspis* sp. nov. occurs with *Redlichops* (q.v.) and there is no independent indication of its horizon. The most similar species, *Realaspis strenoides*, occurs at Los Cortijos, in strata of the Galician-Castilian Zone near Toledo, central Spain (Sdzuy 1961: 594), where it occurs with *Pseudolenus*, *Kingaspis* cf. *velatus*

Sdzuy, 1961, and protolenids, which suggest the Bilbilian Stage (Liñán *et al.*, 1993: 822).

Genus *ONARASPIS* Öpik, 1968

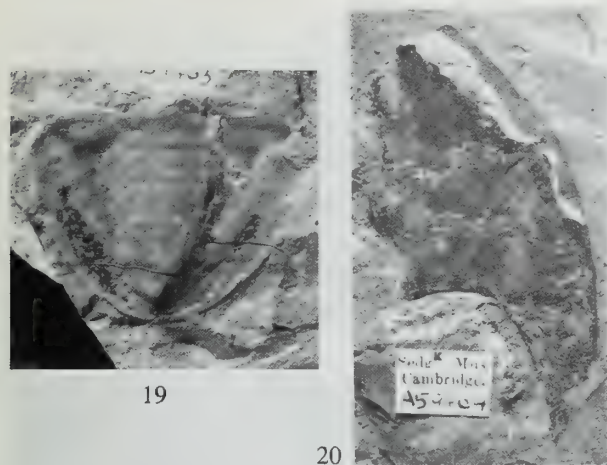
TYPE SPECIES. *Onaraspis somniurna* Öpik 1968, by original designation.

Onaraspis palmeri (Parnes, 1971)

Figs 19, 20

- 1923 Asaphid; King: 511 [briefly described as 'of a distinctly Asaphid type', no figure].
 1971 *Myopsolenus palmeri* Parnes: 202, pls 3, 4 [described].
 1975 *Myopsolenus palmeri* (Parnes); Öpik: 8, 9 [compared with *O. somniurna*; the reference on p. 8 to '*Myopsolenites*' is a misprint].

DISCUSSION. The type material, from Har 'Amram south of the Timna area, is poorly preserved and it is difficult to ascertain the characters of the species. Geyer (1990b: 175) pointed out that Parnes' reconstruction of the cranidium differs in several respects from typical *Myopsolenus*, and suggested instead that it might be a member of the Bathynotidae. Considering the cranidial features, it is more like some *Metadoxides* (Pillola 1991: pl. 10, fig. 6), but the pygidium of *O. palmeri*, which has an axis of several segments and pleural fields with a broad border, is distinct from that of *M. armatus* (Meneghini), well figured by Pillola (1991: pl. 9, fig. 4), and more like that of *Onaraspis*. Öpik (1975: 9) suggested that *Myopsolenus palmeri* was 'the same or . . . closely related' to *O. somniurna*. We



Figs 19, 20 *Onaraspis palmeri* (Parnes), from King's (1923) locality 83, Wadi Rimeileh. **19**, pygidium, external mould, Sedgwick Museum A.59463. **20**, librigena, the infill between dorsal surface and doublure shows white, Sedgwick Museum A.59464. Both unwhitened, $\times 1.3$.

accept the generic reference but the observed differences are probably of specific significance: for example *O. palmeri* has a longer frontal area and the pleural field of the pygidium tapers backwards less strongly.

King's material from Wadi Rimeileh (Figs 19, 20) consists of a large librigena, some pleural fragments and two pygidia, of which one is complete. The specimens are fairly well preserved in siltstone and, though somewhat flattened, show granulose sculpture. The pygidium appears to agree with that of *O. palmeri* but is longer in proportion than that of *O. somniurna*, though it may be more similar to Öpik's (1968: 159) *Onaraspis* sp. A.

HORIZON. Parnes (1971: pls 3, 4) recorded *O. palmeri* from the lower and upper parts of the Timna Formation, respectively from the upper part of the Hakhilil Member at Timna and from beds at Har 'Amram that are correlated with the Mikhrot Member. The specimen from Wadi Rimeileh is from a siltstone interval in the Burj Formation, but its stratigraphical relationship to other localities is unknown.

Superfamily **ELLIPSOCEPHALOIDEA** Matthew, 1887

Family **ELLIPSOCEPHALIDAE** Matthew, 1887

Subfamily **ELLIPSOCEPHALINAE** Matthew, 1887

Genus **KINGASPIS** Kobayashi, 1935

TYPE SPECIES. *Anomocare campbelli* King, 1923, by original designation.

DISCUSSION. Geyer (1990b: 102) placed *Kingaspis* close to *Ellipsocephalus*, regarding the separate family (or subfamily) Kingaspididae (or Kingaspidinae) as superfluous. He discussed the type species, *K. campbelli* (King) and described several other species of *Kingaspis* and of the closely related genus *Kingaspidoides* Hupé, 1953. All species of these genera have features of the cranidium effaced on the external surfaces, but axial and glabellar furrows are generally visible on internal moulds. The weakness of these furrows makes measurements taken from them rather imprecise, hampering morphological comparisons, but the form of the glabella, which has concave sides, expanded anterolateral corners and 4 or 5 pairs of furrows, is consistent.

Kingaspis campbelli (King, 1923)

Figs 21–26

- 1923 *Anomocare campbelli* King: 511, figs 3, 4 [described, illustrated with line-drawings].
- 1935 *Kingaspis campbelli* (sic) (King); Kobayashi: 196, pl. 23, figs 9, 10 [assigned to *Kingaspis*; poor photographs of King's specimens, the cranidium is incorrectly restored].
- 1990b *Kingaspis campbelli* (King); Geyer: 104, pl. 15, fig. 11, pl. 17, figs 8–10 [Moroccan specimens described and discussed, with full synonymy].

MATERIAL. King's syntype material is preserved in the Sedgwick Museum, Cambridge, and from that the cranidium SM A.1311, figured by King (his fig. 3), is here selected as lectotype (Figs 21a–c herein). Topotypic material is held in other museums (Hebrew University of Jerusalem; Senckenberg Museum, Frankfurt; Natural History Museum, London); more recently Dr J. H. Powell collected further specimens, one of which is figured here (Fig. 25).

DISCUSSION. Topotypic material is well preserved and agrees with Geyer's description. He remarked that *K. campbelli* has a relatively wider cranidium (1.3 times the length) than other species of the genus. There is slight variation in transverse convexity and in the evenness of the curvature in sagittal section.

Geyer excluded the pygidium described by King from the species, but because it is the only kind of pygidium found with monospecific associations of the cranidia of *K. campbelli*, King probably originally associated them correctly. King's large paralectotype is shown here (Fig. 22). A smaller well preserved example (Fig. 26) is 5.0 mm long and estimated to have been 13 mm wide; axis more than a quarter of the total width, convex, with 3 axial rings and a trace of a fourth; pleural regions with 4 pleural furrows and three interpleural grooves; border narrows slightly backwards.

Originally described from the Burj Formation at Wadi Zarqa Ma'in, topotypic specimens have since been figured many times (see Geyer 1990b: 104).

HORIZON. At Wadi Zarqa Ma'in *K. campbelli* is in earliest Middle Cambrian beds associated with the lower Amgan species *Palaeolenus antiquus* (Chernysheva), discussed below. In Morocco it is questionably recorded from the *frequens* Zone.

Genus **KINGASPIDOIDES** Hupé, 1953

TYPE SPECIES. *Kingaspidoides armatus* Hupé, 1953, by original designation.

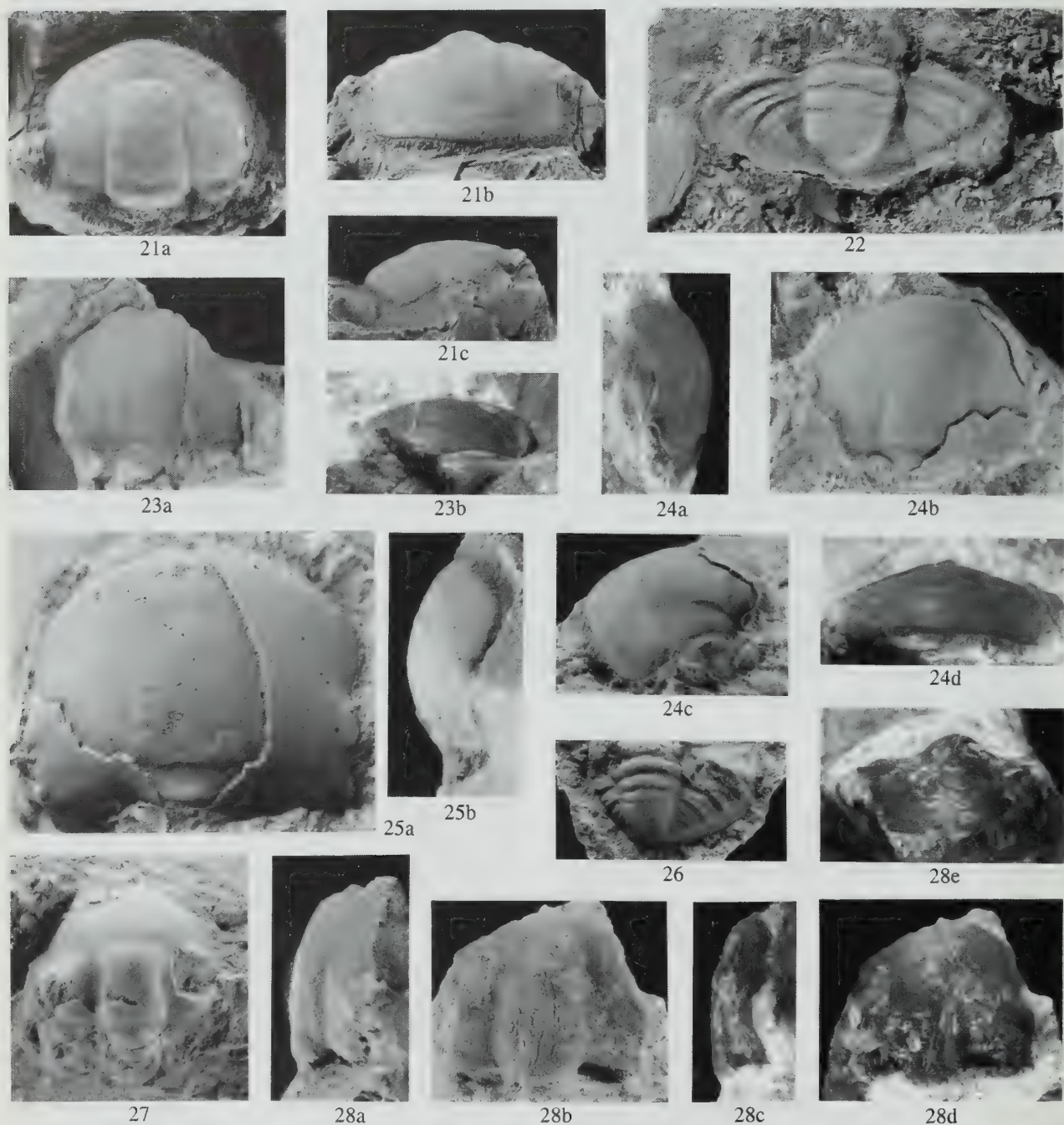
DISCUSSION. *Kingaspidoides* was originally instituted for kingaspidids with an occipital spine (Hupé 1953), but Geyer (1990b: 110) emended the diagnosis and distinguished the genus from *Kingaspis* by the relatively uneven convexity of the cranidium in transverse section.

Kingaspidoides cf. *obliquoculatus* Geyer, 1990 Figs 27, 28

cf. 1990b *Kingaspidoides obliquoculatus* Geyer: 118, pl. 18, figs 1–15.

MATERIAL. Three cranidia from Al Abrash, Ghor-es-Safi, BM In24056-8, collected by Dr A. E. Day in 1909. Associated with *Psiloria dayi* Cooper (1976: 283), for which this is the type locality.

DESCRIPTION AND DISCUSSION. The glabella has independent transverse convexity (Fig. 28e). Interocular area of fixigena scarcely convex, slopes down to palpebral lobe which is short, the posterior end lying well forward of SO. Glabella relatively narrow; at a line



Figs 21–26 *Kingaspis campbelli* (King), Wadi Zarqa Ma'in. **21a–c**, lectotype, top, front and side views of exfoliated cranidium, showing glabella and independent convexity of occipital ring, Sedgwick Museum A.1311, $\times 3$ (figured King 1923: fig. 3). **22**, paralectotype, large pygidium, Sedgwick Museum A.1310, $\times 3$ (figured King 1923: fig. 4a). **23–26** are topotypes; **23a, b**, top and front views of testate cranidium (23b, unwhitened, shows the even transverse convexity of the cranidium), In.22997/1, $\times 3$; **24a–d**, side, top, oblique and front views of partly exfoliated cranidium (24a and 24d, unwhitened, show the even convexity, 24b and 24c show the glabella and frontal border), In.22996, $\times 3$; **25a, b**, top and side views of partly exfoliated cranidium (25a shows the difference between the internal and external surface), It.26231, 25a $\times 4$, 25b $\times 3$; **26**, latex cast of external mould of pygidium, In.22997/2, $\times 3$.

Figs 27, 28 *Kingaspidoides cf. obliquoculatus* Geyer, 'Al Abrash, Ghor-es-Safi' (exact locality uncertain). **27**, internal mould of fragmentary cranidium, In.24058, $\times 3$. **28a–e**, abraded testate cranidium (28a, 28b, side and top views, whitened, showing the independent convexity of the glabella; 28c–e, side, top and front views, unwhitened, showing the course of the facial suture and transverse convexity of the glabella), In.24056, 28a, 28b $\times 3.5$, 28c–e $\times 3$.

through the palpebral lobes it is <40% of cranial width (Fig. 28b). No occipital spine or node. Frontal area relatively long, nearly 25% of cranial length. Surface smooth, but the internal mould shows tiny pits (= granules on the parietal surface of the cranidium) and caeca on the preglabellar field.

Among *Kingaspidoidea* without an occipital spine, *K. obliquoculatus* differs from *K. neglectus* Geyer (1990b: 120) in having a shorter and narrower glabella, and from *K. borjensis* Geyer (1990b: 122) in having a shorter palpebral lobe which does not extend back to the level of SO.

HORIZON. Burj Formation, Ghor-es-Safi. *K. obliquoculatus* was originally described from the Asrir Formation (*Hupeiolenus* Zone) of the Fougara section in the Anti-Atlas Mountains, Morocco.

Family PALAEOLENIDAE Hupé, 1953

DISCUSSION. The Palaeolenidae were discussed and briefly characterised by Geyer (1990b: 67). The glabella is well defined and tends to be clavate and typically shows four pairs of glabellar furrows; the posterior pair (S1) curve slightly inwards and backwards, S2 and S3 are nearly transverse, short and not connected across the glabella, and S4 is short and slightly oblique inwards and forwards. In *Palaeolenus lantenoisi* Mansuy, 1912, the glabella is almost parallel-sided but in *P. douvillei* Mansuy, 1912, the type of the genus, the glabella is slightly clavate; in both those species the preocular sections of the facial suture are approximately parallel. In *P. deprati* Mansuy, 1912, the type species of *Megapalaeolenus* Chang, 1966, the glabella is clavate and the preocular sutures diverge forwards. It is doubtful whether *Megapalaeolenus* should be maintained as an independent genus.

Genus PALAEOLENUS Mansuy, 1912

DISCUSSION. The species described below was originally assigned to the genus *Schistocephalus* Chernysheva, 1956, which has been regarded as a member of the Family Paradoxididae. The distance from the anterior end of the palpebral lobe to the glabella, connected by an eye-ridge, and the presence of a parafrontal band (Fig. 29a), are features of various genera commonly referred to the superfamily Ellipsocephaloidea (Geyer 1990b). The type species of *Schistocephalus*, *S. enigmaticus* Chernysheva (1956: pl. 30, figs 1, 3), has a parallel-sided glabella on which the glabellar furrows S1 to S3 are arched backwards and joined strongly across the mid-line; S4 lies relatively close to S3 and is very short. The anterior part of the glabellar appears transversely oval. Other species of *Schistocephalus* have been described which show rather diverse glabellar morphology (Chernysheva 1971: pls 6, 7). Most of them have a slightly clavate glabellar with a semi-circular frontal lobe; some of them, such as *S. juvenis* Chernysheva, 1956 (Sdzuy 1995: pl. 1, fig. 8) and *S. amzassiensis* Fedjanina (in Chernysheva 1971: pl. 6, figs 8–13), share with *S. enigmaticus* the strongly transglabellar furrows S2 and S3. See also *S. ex gr. juvenis* well figured in Egorova *et al.* (1976: pls 32–34). In some other early species such as *S. antiquus* Chernysheva, 1956, and *S. tchernyshevae* Bognibova (in Chernysheva 1971) these furrows do not join across the glabella. The latter forms are closer in this feature to *Palaeolenus* (especially species that have been referred to *Megapalaeolenus*) and it seems appropriate to transfer them to that genus rather than extend *Schistocephalus* unduly. Chu (1962) suggested that *Palaeolenus* is ancestral to *Schistocephalus*.

Ferralsia Cobbold (1935) is very similar to *Palaeolenus*, but

Geyer & Elicki (1995: 112), who reviewed *Ferralsia*, maintained that it could be distinguished from *Palaeolenus* by its shorter and more regularly spaced glabellar furrows; in at least some species of *Palaeolenus* S3 and S4 are closer together than S1 and S2. Furthermore, *Ferralsia* tends to have a longer preglabellar field and narrower interocular fixigenae. However, in view of the variation shown by species of *Palaeolenus* and *Schistocephalus*, these features, even if they are considered to be of generic value, may be difficult to apply.

It is possible that the genus *Gigoutella* Hupé, 1953, would be an appropriate reference for some of those taxa with discontinuous glabellar furrows, but regrettably the genus is known only from a single schematic line-drawing (which is misleading according to Geyer & Elicki 1995: 112). As attempts to examine the original material have been unsuccessful, the nature and relationships of the only described species, *G. atlasensis* Hupé (1953), remain to be elucidated, but it may prove to be a senior synonym of *Megapalaeolenus* (and, following Sdzuy (1995), *Schistocephalus* if a broad view is taken of that genus), or a junior synonym of *Ferralsia*.

Palaeolenus antiquus (Chernysheva, 1956) Figs 29–38

- 1956 *Schistocephalus antiquus* Chernysheva: 150, pl. 30, fig. 6 [cranidium figured, compared with *S. enigmaticus*].
 1976 *Schistocephalus antiquus* Tchernysheva [sic]; Egorova *et al.*: 74, pl. 23, figs 11–14, pl. 25, figs 1, 2, pl. 28, fig. 1 [figures of several cranidia].
 1995 *Schistocephalus antiquus* Chernysheva; Sdzuy: pl. 1, fig. 9 [new figure of holotype].

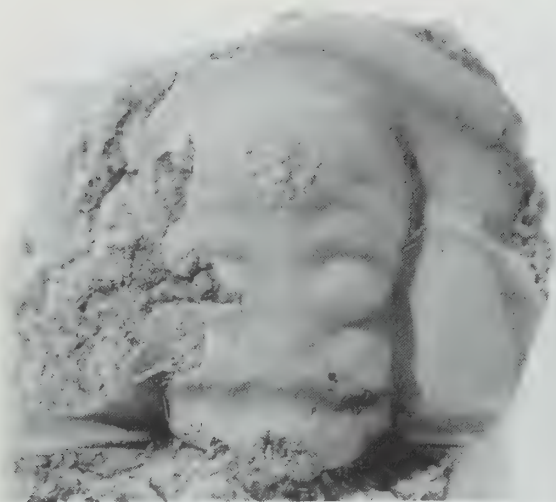
NEW MATERIAL. Sixteen cranidia (mostly fragmentary), two librigenae and three small pygidia, all from a calcarenite bed (Fig. 6) in a culvert, 0.8 km N of Wadi Zarqa Ma'in (BM It26214–30).

DESCRIPTION. Glabella (including occipital ring, LO) clavate, occupies 85% of cranial length; forward of L2 widens to a maximum opposite S4, where it is about 120% of the width of L1. Glabellar lobes L1 to L4 become progressively shorter (exsag.); the frontal lobe is well rounded anteriorly. LO without node. S1 slightly curved inwards and backwards, with a tendency to bifurcate medially; S2 approximately transverse but each furrow forms a slight convex curve anteriorly; S3 similar to S2 but extends inwards and slightly forwards; S4 shorter than S3, curved or more anteriorly directed. Anterior border has terrace-lines parallel to margin and is a little longer sagittally than preglabellar field. Preocular section of facial suture diverges forward at about 30° to sagittal line. Palpebral lobe one-third of cephalic length, continuous with eye-ridge which reaches glabella opposite S4 and extends forward into a narrow parafrontal band, seen on some specimens (Figs 29a, 34). Interocular area of fixigena about two-thirds of glabellar width at S1. Postocular area of fixigena not quite as wide as LO. Exterior surface granulose, most coarsely so on the median part of the glabella and the interocular fixigena, more finely on the preocular fixigena. Internal mould almost smooth, very finely pitted, indicating very fine granulation on the parietal surface of the exoskeleton.

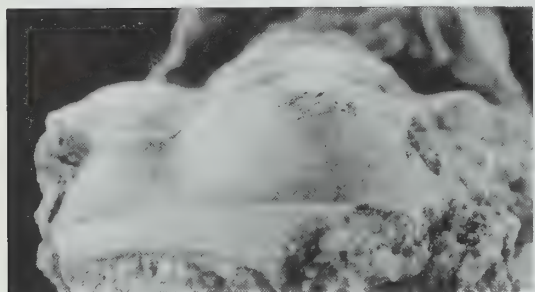
Librigena narrow, the border occupying nearly half the total width. Genal spine very short (Fig. 36).

Pygidium small, with wide short axis having one distinct and one faint axial ring. Pleural field very small with one pleural furrow and two faint interpleural grooves (Fig. 33).

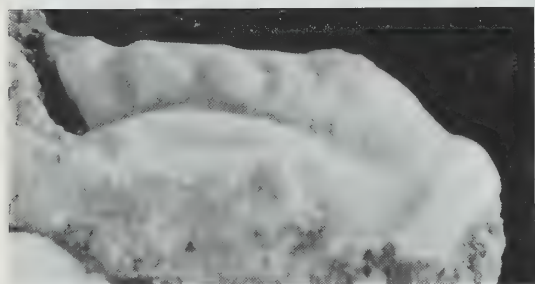
DISCUSSION. The specimens from Wadi Zarqa Ma'in agree closely with the holotype and also the specimens figured by Egorova *et al.* (1976), except that the interocular fixigena is a little wider in some of the Jordanian specimens; the glabella widens forward less than in the holotype (Sdzuy 1995: pl. 1, fig. 9), but more than some of the



29a



29b



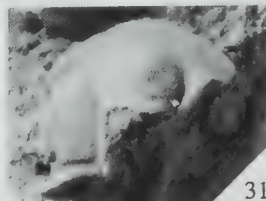
29c



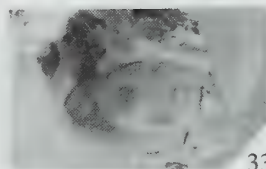
37



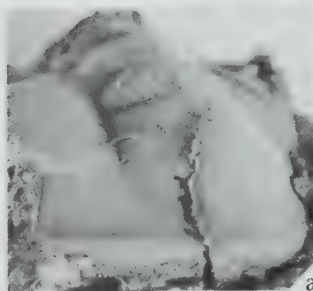
30



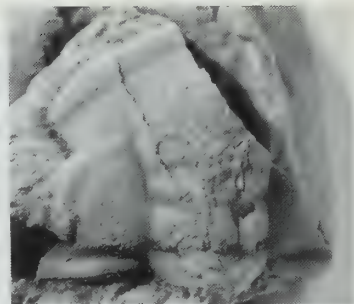
31



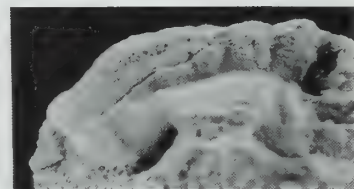
33



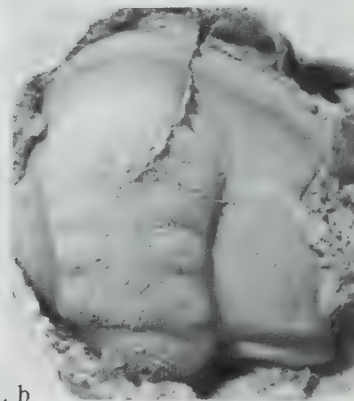
a



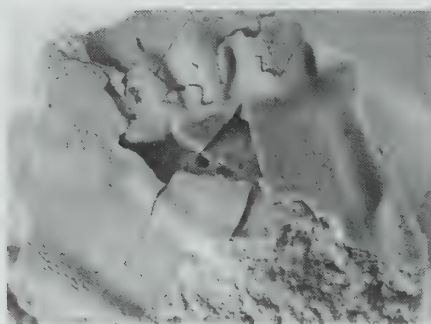
32a



32b



b



35



36



38

other figured specimens (Egorova *et al.* 1976: pl. 23, fig. 11, pl. 25, fig. 1). Granulate sculpture is not seen in the holotype but is shown by Egorova *et al.* (1976: pl. 28, fig. 1).

Palaeolenus tchernyshevae (Bognibova in Chernysheva 1971: pl. 7, figs 6, 7, 9–12) differs from *P. antiquus* in having a narrower border and lacking a preglabellar field, so that the glabella occupies well over 90% of the cranial length. The pygidia assigned to the two species are much alike.

Among species described from China the most similar is *Palaeolenus fengyangensis* Chu, 1962, which has an expanded glabella and divergent preocular sections of the facial suture, and has been referred to *Megapalaeolenus*. Figured material (Chu 1962; Zhang *et al.* 1980: pl. 72, figs 6–8) is of smaller cranidia than our material, but the glabella appears proportionately wider, there is a small occipital node and the preocular sutures are less divergent; the surface is not recorded as granulose.

HORIZON. *Palaeolenus antiquus* is recorded from the *antiquus* Zone at the base of the Amgan Stage in sections on the rivers Lena and Amga in eastern Siberia, and extends into the base of the overlying *Kounamkites* Zone (Egorova *et al.* 1976, table, p. 14); it occurs in carbonate deposits, in contrast to such species as *S. amzassensis* Fedjanina and *S. impressus* Fedjanina (both in Chernysheva 1971), which are recorded from clastic deposits (Chernysheva 1971: table, column 1). Species retained in *Schistocephalus* (*S. enigmaticus*, *S. juvenis*) are recorded from higher horizons (Chernysheva 1971).

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Figs 29–38 *Palaeolenus antiquus* (Chernysheva). Wadi Zarqa Ma'in. **29a–c**, top, front and side views of exfoliated cranidium, showing parafrontal band. It.26214, × 4. **30–32**, small cranidia showing external surface, × 4; **30**, It.26222; **31**, It.26221; **32a, b**, top and side views of It.26216. **33**, pygidium, It.26228, × 6. **34a, b**, latex cast of external mould, oblique and top views, It.26217, × 4. **35**, fragmentary cranidium showing sculpture of fixigena, It.26218, × 4. **36**, small librigena, It.26226, × 5. **37**, fragment of large cranidium, showing glabellar furrows: the internal mould is finely pitted, It.26215, × 4. **38**, fragment of cranidium, showing palpebral lobes and postocular facial suture, It.26220, × 4.

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The first Palaeozoic rhytidosteid: *Trucheosaurus major* (Woodward, 1909) from the Late Permian of Australia, and a reassessment of the Rhytidosteidae (Amphibia, Temnospondyli)

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SYNOPSIS. A restudy of *Bothriceps major*, a temnospondyl from the Late Permian of Australia, has resulted in a new taxonomic assignment of the specimen. The species is returned to *Trucheosaurus* and the specimen is recognized as a rhytidosteid, rather than a brachyopid. Thus, it constitutes the first Palaeozoic record of the Rhytidosteidae, which has long been considered to be restricted to the Early Triassic. A phylogenetic analysis of all taxa previously included in the superfamily Rhytidosteoidea was performed. One monophyletic group, the family Rhytidosteidae, is recognized, but the relationships of most taxa within that clade remain unresolved.

INTRODUCTION

In 1909, Woodward described a new Australian brachyopid taxon, *Bothriceps major*, based on a specimen collected in Late Permian deposits from the Sydney Basin (New South Wales). The genus was previously erected by Huxley (1859) for an Australian brachyopid, *B. australis*, represented by a single skull of unknown provenance (Watson 1919, 1956; Welles & Estes 1969; Warren 1997). Subsequently, Watson (1956) restudied *B. major* and referred the specimen to a new genus of brachyopid, *Trucheosaurus*, largely because 'in the few structures clearly shown in the only known specimen it differs from the type of the genus *Bothriceps* and indeed from all other known genera of the family', and also because 'the specimen is important as showing the occurrence of a typical brachyopid at an early horizon'. Subsequently, Cosgriff (1969) presented a brief redescription of *T. major* based on his own observation of part of the type material (MMF 12697), and also discussed the age of the specimen. Welles & Estes (1969) argued that the new genus, *Trucheosaurus*, could not be justified, so they returned the species to *Bothriceps*.

The holotype material of *B. major* consists of a poorly preserved specimen which includes the skull and a partial articulated postcranial skeleton. At present, the specimen comprises four pieces distributed in three different repositories: the skull (MMF 12697a) is in the Geological Survey of New South Wales (Sydney), the postcranial skeleton (AMF 50977) in the Australian Museum (Sydney), and the counterpart of both skull and postcranial skeleton (BMNH R3728) in the collections of The Natural History Museum, London.

The present paper is a redescription and a reassessment of the taxonomic position of *B. major* based on a re-evaluation of the entire holotype material. It was prompted during our joint study of the material in 1995 when the Australian part of the skull was further prepared, revealing an extended quadratojugal area on the left hand side. The specimen then assumed a triangular shape, with the

posterior margin apparently lacking both tabular projections and otic embayment, a morphology found in several members of the family Rhytidosteidae. A few patches of rhytidosteid ornament were also present. *Bothriceps major* is returned to Watson's available taxon, *Trucheosaurus*, and included in the family Rhytidosteidae. A preliminary phylogenetic analysis of the family Rhytidosteidae is presented and the position of the taxon discussed in a cladistic context.

SYSTEMATIC PALAEONTOLOGY

TEMNOSPONDYLI Zittel, 1888

Family RHYTIDOSTEIDAE Huene, 1920

Genus *TRUCHEOSAURUS* Watson, 1956

TYPE SPECIES. *Bothriceps major* Woodward 1909; Late Permian (Dzhulfian), Sydney Basin, New South Wales, Australia.

DIAGNOSIS. As for the type and only species.

Trucheosaurus major (Woodward 1909) Figs 1–6

- 1909 *Bothriceps major* Woodward: 319, pl. LI.
- 1956 *Trucheosaurus major* (Woodward); Watson: 327–330, fig. 3.
- 1969 *Bothriceps major* Woodward; Welles & Estes: 22.
- 1969 *Trucheosaurus major* (Woodward); Cosgriff: 80.
- 1972 *Trucheosaurus major* (Woodward); Howie: 269.
- 1973 *Trucheosaurus major* (Woodward); Cosgriff: 1095–1100.
- 1974 *Trucheosaurus major* (Woodward); Cosgriff: 94.
- 1977 *Bothriceps major* Woodward; Chernin: 88.
- 1981 *Bothriceps major* Woodward; Warren: 273.
- 1997 *Bothriceps major* Woodward; Warren: 27, fig. 3.

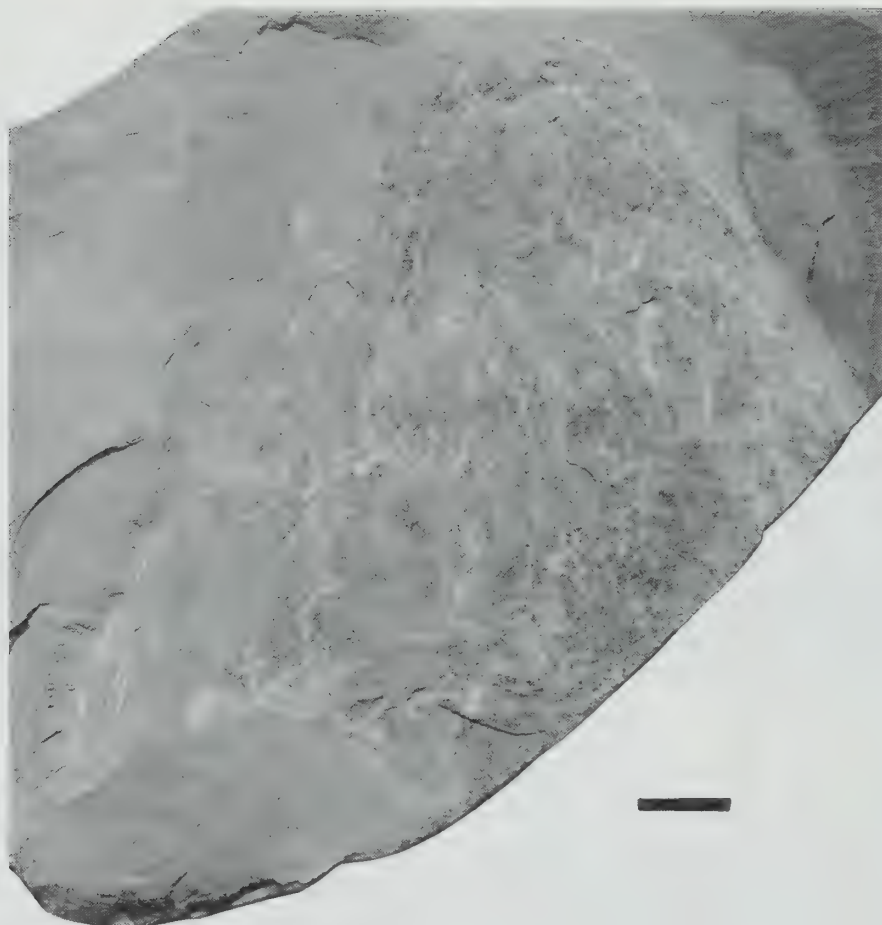


Fig. 1 *Tracheosaurus major*, holotype MMF 12697a. Skull. Scale bar represents 20 mm.

DIAGNOSIS. Rhytidosteid amphibian apparently lacking tabular projections and otic notch; markedly small orbits located laterally on the anterior third of the skull table; extremely anteroposteriorly elongated parietal bones, which are nearly three times the length of the frontals and apparently without pineal foramen.

HOLOTYPE. Skull table (MMF 12697a), the partially complete and articulated postcranial skeleton (AMF 50977), and the counterpart of both skull and postcranial skeleton (BMNH R3728).

TYPE LOCALITY AND HORIZON. Glen Davis Formation of the Charbon Subgroup, the lower deltaic facies of the Illawarra Coal Measures, Airly, near Capertee in the west of the Sydney Basin (New South Wales, Australia). The whole of the Illawarra Coal Measures are Late Permian (Young & Laurie 1996). The Glen Davis Formation, which is placed mid-way through the Illawarra Coal Measures (McMinn 1985), contains the palynomorph *Microreticulatisporites bitriangularis*, the index form for the base of the APP5.2 Interval Zone (Burger *et al.* 1992), making it middle Dzhulfian. This Dzhulfian correlation for the middle part of the Illawarra Coal Measures was confirmed in the most recent survey of evidence for the placement of the Permo-Triassic boundary in Australia (Foster *et al.* 1997).

DESCRIPTION

Skull. As mentioned above, the specimen is only preserved as a thin layer of bone on two slabs (part and counterpart). Although obvi-

ously part and counterpart of the same specimen, the two halves do not meet cleanly when fitted together as several millimetres of the bone is missing in places.

Determining sutures was difficult as little detail remains, perhaps because the specimen was preserved in a torbanite. The clearest sutures are in the area of the left tabular, postparietal, supratemporal, parietal, postfrontal and postorbital. The other sutures were delineated following the pattern of the bone radiation, although in the anterior snout region sutures remain fairly unclear. Suture lines were traced with chalk on the part and counterpart (Figs 1, 2) and the specimens drawn (Figs 3, 4). The drawings were then superimposed and the skull redrawn as a composite (Fig. 5). The main problem encountered during our restoration was determining the position of the orbits, which have been restored in the only possible place. The nostrils are marked by raised areas. Apparent ornamentation preserved is faint but seems to show a delicate and smooth spider-web pattern with small nodes on the ridges.

The skull table is nearly straight sided, with the posterior margin lacking both tabular projections and otic embayment. The orbits must have been very small, and located laterally on the anterior third of the skull table. There is no sign of a pineal foramen. A striking feature of the specimen is the extremely anteroposteriorly elongated parietal bones, which are nearly three times longer than the frontals. Apparently, there is no lachrymal bone.

Part of the occiput is visible behind the posterior border of the



Fig. 2 *Tracheosaurus major*, holotype BMNH R3728. Skull. Scale bar represents 20 mm.

skull table, presumably owing to the dorso-ventral compression of the specimen. A slender left paroccipital process is the best preserved part of the skull. It shows a clear tabular-exoccipital suture close to the area of the exoccipital condyle. Part of the descending portion of the left postparietal is also preserved. Posteriorly to the postparietals, a layer of bone is present and presumably could be either part of the palate (? parasphenoid) or part of the pectoral girdle (? interclavicle). It has been omitted from the figures but can be seen in the photographs (Figs 1, 2).

On the posterior left corner of the skull, a fragment of bone projects behind the putative quadratojugal. It either represents part of an extension of the quadratojugal or is part of the mandible. In Fig. 5, we have restored it as a quadratojugal.

Postcranial skeleton. Parts of the right fore and hind limb and at least 31 presacral and postsacral centra are preserved, with accompanying ribs (Fig. 6).

The condition of the vertebrae is such that they are most easily counted by means of the clearly defined ribs. In the anterior part of the column the section is frontal, with both left and right ribs from 21 centra preserved. More posteriorly, a flake of torbanite containing 5 ribs is missing from the right side. Following this,

the section changes so that it preserves part ribs, only, on the left and seven apparent centra with accompanying neural arches on the right. Next are three structures which resemble swept back neural spines from a tail fin with the final two vertebrae represented by poorly defined centra. The column is certainly rhachitinous in the caudal region but could be rhachitinous or stereospondylous more anteriorly.

The ribs themselves are shorter than usual for temnospondyls. In the anterior part of the column they are curved but the curvature is not preserved posteriorly. No indication of uncinat processes is present on any rib.

The humerus, radius and ulna of the right fore limb are partially preserved close to their expected position, as are several other small displaced elements. Two long bones either side of the vertebral column in this area may be the remains of a displaced left fore limb or partial pectoral girdle elements. The right hand element was labelled 'x' by Woodward (1909).

More posteriorly, several patches of bone are preserved on the right and may be the tibia and fibula of both hind limbs as well as some metapodials. There is no sign of the femora.

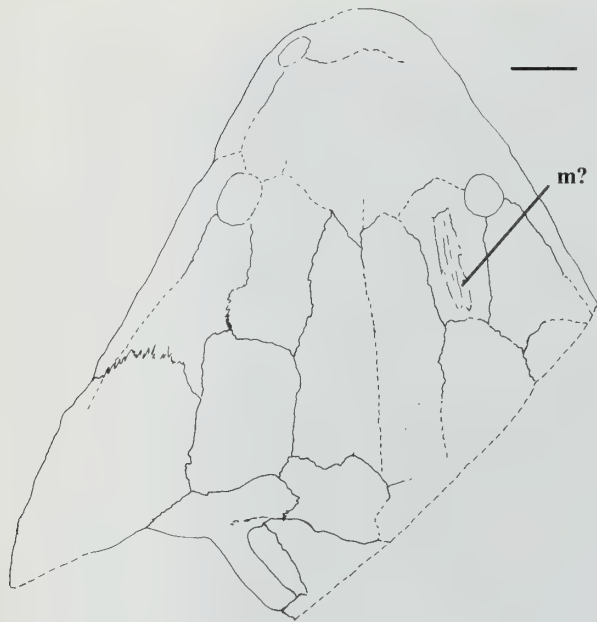


Fig. 3 *Tracheosaurus major*, holotype MMF 12697a. Diagram of skull from Fig. 1. Scale bar represents 20 mm. m?, possible mandibular fragment.

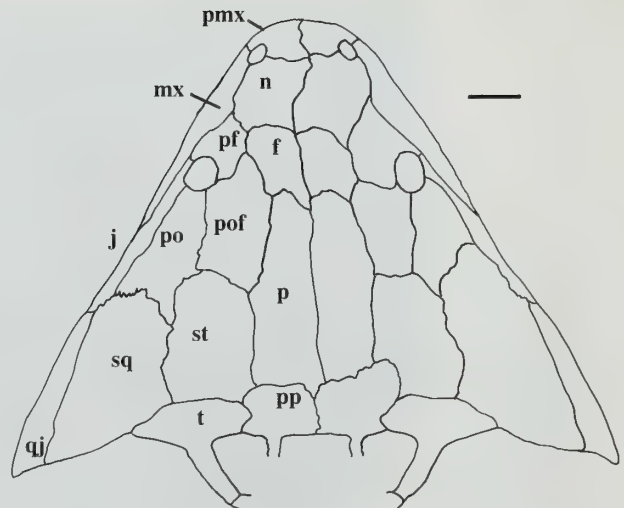


Fig. 5 *Tracheosaurus major*. Drawing of the skull incorporating only those parts preserved on MMF 12697 and BMNH R3728. No attempt has been made to correct probable flattening of the skull or to speculate on the original shape of the occiput. It is unlikely that the paroccipital process of the tabular and exoccipital protrudes posteriorly in the undistorted specimen. Scale bar represents 20 mm. f, frontal; j, jugal; mx, maxilla; n, nasal; p, parietal; pf, prefrontal; pmx, premaxilla; po, postorbital; pof, postfrontal; pp, postparietal; qi, quadratojugal; sq, squamosal; st, supratemporal; t, tabular.

PHYLOGENETIC ANALYSIS

The family Rhytidosteidae was erected by Huene (1920) for *Rhytidosteus* and *Peltostega*. Later, Cosgriff (1965) created the superfamily Rhytidosteoidea for the Rhytidosteidae and the monogeneric family Laidleridae (Kitching 1957). Subsequently, Cosgriff & Zawiskie (1979) removed the Laidleridae and erected a new rhytidosteid family, the Indobrachiopidae, for those members of the Rhytidosteidae with rounded, as opposed to triangular, skulls. Because they were unable to distinguish the families Rhytidosteidae and Indobrachiopidae except on the basis of skull outline, Warren & Black (1985) returned the members of the Indobrachiopidae to the Rhytidosteidae. Shishkin (1994) re-erected the Rhytidosteoidea, including in it the Rhytidosteidae and Peltostegidae. More recently, Warren (1998) restricted the superfamily to the Rhytidosteidae and Laidleridae.

The purpose of this preliminary analysis is to provide a hypothesis for the relationships among rhytidosteids and determine whether more than one monophyletic group is represented. Nearly all those characters used in the different revisions mentioned above were considered. Nevertheless, the triangular shape of the skull, although it was used in all previous diagnoses of the family, was not included as it was not possible to define discrete states for this character, especially in the case of incomplete material.

The following rhytidosteid taxa were used in the analysis: *Rhytidosteus capensis* (Owen 1884, Cosgriff 1965), *Peltostega* sp. (Nilsson 1946), *Laidleria gracilis* (Kitching 1957, Warren 1998), *Indobrachiops panchetensis* (Heune & Sahni 1958, Cosgriff & Zawiskie 1979), *Deltasaurus kimberleyensis* (Cosgriff 1965), *Rewana quadricuneata* (Howie 1972), *Derwentia warreni* (Cosgriff 1974), *Arcadia myriadens* (Warren & Black 1985), *Boreopelta vavilovi* (Shishkin & Vavilov 1985), *Mahavisaurus* sp. (Lehman



Fig. 4 *Tracheosaurus major*, holotype BMNH R3728. Diagram of skull from Fig. 2. Scale bar represents 20 mm.



Fig. 6 *Tracheosaurus major*, holotype AMF 50977. Postcranial skeleton. Scale bar represents 50 mm.

1966, Cosgriff & Zawiskie 1979), *Pneumatostega potamia* (Cosgriff & Zawiskie 1979), *Acerastea wadeae* (Warren & Hutchinson 1987) and *Trucheosaurus major*. The lydekkerinid taxa *Lydekkerina* (Parrington 1948) and *Chomatobatrachus* (Cosgriff 1974) and the family Trimerorhachidae (Broom 1913, Olson 1955) were considered as outgroups, taking into account previous cladistic analyses of the Temnospondyli (Milner 1990, 1991). All terminal taxa used in the analysis were examined by one or both of the authors. The taxon-character state matrix (Table 1) and character list are included in the Appendix.

DISCUSSION. The incorporation in the analysis of several taxa represented by poorly preserved specimens greatly increased the instability of the resultant cladogram, and thus the number of equally parsimonious trees. Under these circumstances, four taxa were excluded from the analysis, reducing the number of terminals to twelve. Taxa excluded were: *Mahavisaurus* sp., *Pneumatostega potamia*, *Acerastea wadeae* and *Trucheosaurus major*, and their relationships are discussed separately. Accordingly, the phylogenetic results are based on an analysis of 18 characters and 12 terminal taxa, using Swofford's (1993) PAUP 3.1. The branch-and-bound search algorithm resulted in 51 equally-parsimonious trees with a tree length of 23 steps (CI = 0.83 and RI = 0.89). Fig. 7 depicts the strict consensus tree, showing the consistent nodes among the 51 trees.

The monophyletic group (*Indobrachyops* + (*Boreopelta* + *Derwentia* + *Laidleria* + *Peltostega* + (*Rhytidosteus* + *Deltasaurus*) + *Rewana* + *Arcadia*)), that we consider the family Rhytidosteidae (Fig. 7, node 1), is supported by the following eight unequivocal synapomorphies: orbits located close to the skull margin (1); otic notch reduced or absent (3); tabular horns reduced or absent (4); straight posterior margin of the palate (7); otic flange absent (8); 'pockets' on the parasphenoid absent (11); cultriform process of the parasphenoid broad and flat (14) and exoccipital condyles horizontally elongated (16). Two further derived character states of this clade are: the presence of a 'twisted' quadrate ramus of the pterygoid (10), and a reduced palatal tooth row (17), although the former reverses in *Derwentia* and the latter reverses in *Peltostega* and *Laidleria*. The derived condition of character 18 (presence of shagreen on all bones of the palatal series) has long been used as a diagnostic family

character (Cosgriff & Zawiskie 1979, Warren & Black 1985, Warren & Hutchinson 1987, Shishkin 1994). In the present analysis, this derived character state justifies a more inclusive group which includes the Tasmanian 'lydekkerinid' *Chomatobatrachus*. Moreover, among rhytidosteids, the shagreen is reduced in *Derwentia* and apparently absent in *Laidleria*. The condition present in *Indobrachyops* for characters 7, 8 and 16 is unknown, and their derived states might justify a less inclusive group excluding *Indobrachyops*. Within Rhytidosteidae, *Indobrachyops* is the sister group of an unresolved clade which includes all the remaining rhytidosteid taxa: (*Boreopelta* + *Derwentia* + *Laidleria* + *Peltostega* + (*Rhytidosteus* + *Deltasaurus*) + (*Rewana* + *Arcadia*)) (Fig. 7, node 2). This monophyletic group is justified by two unequivocal derived character states: skull sculpture with nodules or pustules (5) and lachrymal bone absent (6), although the condition present in *Boreopelta* and *Peltostega* for the latter is unknown. Another synapomorphy of this clade is equivocal: the condition of a contact between the palatine and vomer lateral to the choana (15), which is unknown in *Rewana*, *Boreopelta* and *Peltostega*, and reverses in *Derwentia* and *Arcadia*. Within the clade, the sister-taxon relationship between the South African *Rhytidosteus* and the Australian *Deltasaurus* (Fig. 7, node 3) is justified by the derived condition of characters 12 (exoccipital-ptyergoid suture visible in palatal view) and 17 (palatal tooth row absent). Also, the Australian taxa *Rewana* and *Arcadia* form a clade (Fig. 7, node 4), justified by the presence of a strikingly low ascending ramus of the pterygoid (9) and the presence of the quadrate condyles well behind the occipital ones (13). It is important to remark that the Australian taxa *Arcadia*, *Rewana* and *Derwentia* share the derived condition of character 2 (the orbits in the anterior half of the skull table); however, as the presence of this condition is unknown in some of the members of the in-group (*Boreopelta* and *Peltostega*), it appears in the analysis as an equivocal synapomorphy of the (*Rewana* + *Arcadia*) clade.

Although not included in the analysis, the taxa *Mahavisaurus*, *Pneumatostega*, *Acerastea* and *Trucheosaurus* are considered rhytidosteids and in a more derived position than *Indobrachyops*. This position is supported by the presence in those taxa of a skull sculpture with nodules or pustules, and the absence of lachrymal bones. Both *Acerastea* and *Trucheosaurus* appear to be more closely related to the other Australian taxa through the presence of the orbits in the anterior half of the skull, a condition especially marked in

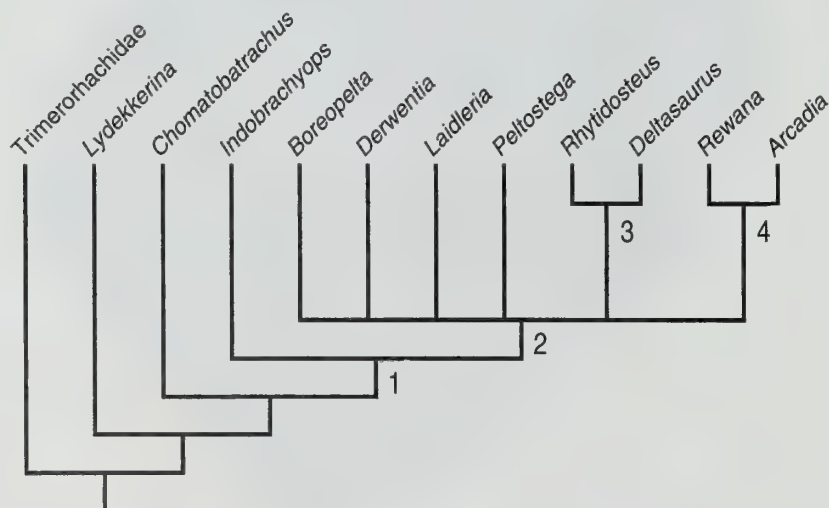


Fig. 7 Strict consensus cladogram of 51 equally parsimonious trees.

Tracheosaurus, and the position of the quadrate condyles behind the occipital ones, visible only in *Acerastea*.

The lack of resolution of most of the generic relationships in the analysis performed herein is apparently due to both the low number of informative characters and the amount of missing entries, which contribute substantially to the instability and poor resolution of the resultant cladogram (Novacek 1992). This result reflects the lack of consensus among investigators concerning the taxonomic validity and content of Rhytidosteoidea and its included families, a problem which has been debated over the last thirty years (see above). This situation strongly indicates that a redescription and further preparation of some specimens is needed, and in many cases the discovery of new, more complete material would improve the resolution of the analysis. Nevertheless, and as a result of the present analysis, most of the Australian taxa (*Arcadia*, *Rewana*, *Acerastea*, *Tracheosaurus*, and *Derwentia*) appear more closely related than they are to other members of the family. The only exception is the Australian taxon *Deltasaurus*, which appears as the sister-taxon of *Rhytidosteus*, from the South African Karoo.

The fact that *Tracheosaurus* is considered here to be a rhytidosteid taxon rather than a brachyopid, constitutes the first Palaeozoic record of Rhytidosteoidea, a family which has long been considered to be restricted to the Early Triassic (Scythian) and because of this used in a biostratigraphic sense (Cosgriff 1969, 1984; Shishkin 1994). Conversely, Brachyopidae no longer has a Permian representative and is thus restricted to the Mesozoic. A second brachyopid, *Bothriceps australis*, was considered to be Permian but only because of its taxonomic relationship with *Tracheosaurus major*, and is most likely Triassic (Warren 1997).

When a phylogenetic hypothesis is combined with the observed fossil record of the terminal taxa, stratigraphic separation between sister-taxa demands substantial range extensions beyond those predicted by the observed stratigraphic record ('ghost lineages' of Norell 1992). Thus, the age of *Tracheosaurus* and its position on the cladogram extend the rhytidosteid diversification and preceding nodes into the Late Permian. Equally, if a more inclusive cladistic analysis of temnospondyls is considered (e.g. Milner 1990), the resultant calibrated phylogeny (Norell 1992) suggests that the phyletic diversification of Mesozoic temnospondyls ('stereospondyls') occurred earlier than indicated by the fossil record. The implication is that the apparent radiation of taxa in the Early Triassic was an extension of a Late Permian event, which probably took place in Gondwana as the earliest and most diverse of the Triassic temnospondyls faunas occur in that area. Therefore, the seeming abruptness of the Permo-Triassic temnospondyl turnover (Milner, 1990: fig. 15.3) might be both an effect of the lack of recent revisions of the known temnospondyl record and its interpretation relative to testable phylogenetic patterns, and a taphonomic artifact. The taphonomic effect may result from the absence of preserved temnospondyl-bearing sequences in the Late Permian, or the preservation of fauna from selected sequences only, as appears to have been the case in South Africa.

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APPENDIX

Character List for Table 1

- Position of the orbits I. The position of the orbits in relation to the skull margins: close to the skull midline (0); close to the skull margin (1).
- Position of the orbits II. The position of the orbits in relation to the skull table length: approximately in the middle (0); in the anterior half of the skull table (1).
- Otic notch: incised (0); reduced or absent (1).
- Tabular horns: well developed and posteriorly projected (0); reduced to a broad based triangle or absent (1).
- Sculpture: 'normal' ridge-grooved pattern without pustules or nodules on the junctions (0); spider-web pattern with nodules or pustules on the junctions (Cosgriff & Zawiskie 1979) (1).
- Lacrimal bone and lacrimal flexure of infraorbital sensory canal: present (0); absent (1).
- Posterior margin of the palate embayed (0); almost straight (1).
- Pterygoid otic flange (= oblique ridge): present (0); absent (1).
- Pterygoid ascending ramus. In those pterygoids without an otic flange, the ascending ramus is a thin lamina that runs along the dorsal surface of the quadrate ramus of the pterygoid and across the corpus: extremely low (1); not extremely low (2).
- Pterygoid quadrate ramus: evenly curved from the horizontal to the vertical plane throughout its length (0); horizontally oriented proximally and vertically oriented distally so it appears twisted (1).
- Ventral depressions on the parasphenoid corpus ('pockets' of Watson 1962): present (0); absent (1).
- Exoccipital-ptyergoid suture: not visible in palatal view (0); visible in palatal view (1).
- Quadrate condyles: well behind the occipital condyles (0); in the same transverse line as the occipital condyles (1).
- Cultriform process of the parasphenoid: narrow (0); broad and flat (1).
- Vomer-palatine contact external to the choana so the maxilla is excluded from its border: absent (0); present (1).
- Exoccipital condyle articular surface: rounded (0); oval and horizontally elongated (1).
- Palatine tooth row: continuous over the palatine series (0); reduced, so it is only partially present on some of the palatal bones (1); absent (2).
- Shagreen: reduced so it appears on some of the palatal series only, not including the tooth bearing bones (0); on the palatal series including the tooth bearing bones (1).

Table 1 Taxon-Character state matrix. The matrix includes 12 taxa and 18 characters. Data missing as a result of lack of preservation or because the state is unknown is coded as '?'. Data unknown but as a result of transformation is coded as '—'. The data matrix was subjected to parsimony analysis using PAUP branch-and-bound option.

TAXA	CHARACTERS																	
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
Trimerorhachidae	0	0	0	0	0	0	0	0	—	0	0	0	0	0	0	?	0	0
Lydekkerina	0	0	0	0	0	0	0	0	—	0	0	0	1	0	0	0	0	0
Chomatobatrachus	0	0	0	0	0	0	0	0	—	0	0	0	1	0	0	0	0	1
Rhytidosteus	1	0	1	1	1	1	1	?	?	?	1	1	1	1	1	1	2	1
Peltostega	1	?	1	1	1	?	1	1	2	1	1	0	1	1	?	1	?	?
Laidleria	1	0	1	1	1	1	1	1	2	1	1	0	1	1	1	1	1	0
Indobrachyops	1	0	1	1	0	0	?	?	?	1	1	0	1	1	0	?	1	1
Deltasaurus	1	0	1	1	1	1	1	1	2	?	1	1	1	1	1	?	2	1
Rewana	1	1	?	?	1	1	1	1	1	?	?	?	?	1	?	1	1	1
Derwentia	1	1	1	1	?	1	1	1	2	0	1	0	1	1	0	1	1	0
Arcadia	1	1	1	1	1	1	1	1	1	?	?	?	0	?	0	1	1	1
Boreopelta	1	?	1	1	1	?	1	1	2	1	1	0	1	1	?	1	?	1

The rhynchonellide brachiopod *Isopoma* Torley and its distribution

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SYNOPSIS. The Devonian rhynchonellid brachiopod genus *Isopoma* Torley, 1934, is described, with comments on species recorded from various geographic regions. *Isopoma maymyoensis* sp. nov. is erected for some specimens from the Late Eifelian to Early Givetian Padaukpin beds of Burma. *Isopoma* is mainly Eifelian to Givetian, Middle Devonian, in age. There are two species in the Pragian and Emsian, Lower Devonian, but possible occurrences in the Frasnian, Upper Devonian, have yet to be proved. Biogeographically the genus belongs to the Rhenish-Bohemian Region of the Old World Realm and has Rhenish affinities.

INTRODUCTION

Having discovered specimens of *Isopoma* Torley, 1934, incorrectly identified, we determined to investigate this poorly known genus to determine its stratigraphic and biogeographic distribution. One of us had previously identified the genus in north Spain (Mohanti, 1972) and, while investigating that fauna, studied specimens of *Isopoma* from various localities in Germany housed at the Senckenberg Natural History Museum at Frankfurt.

MATERIAL

We have studied specimens representing *Isopoma brachyptyctum* (Schnur), *I. gryps* Schmidt, *I. orthoglossa* (Torley), *I. ? ren* Schmidt, and *I. xestum* Torley from the Devonian of Germany, as indicated under the species descriptions. We have also studied specimens in the collections of the Natural History Museum, London, including specimens of *Rhynchonella? lummatoiensis* Davidson, 1865, which we assign to *Isopoma* and for which a lectotype is selected, and the collections from Burma figured and described by Anderson, Boucot & Johnson (1969). Some specimens in this collection identified as *Uncinulus subsignata* (Reed), are described here as *Isopoma maymyoensis* sp. nov. Mohanti also studied *Isopoma hertae* from the Cantabrian Mountains, Spain, housed in the National Natural History Museum, Leiden, Netherlands, which he had described in 1972. Our comments on other species of *Isopoma* are based largely upon information from the literature.

SYSTEMATIC DESCRIPTIONS

Most of the material described here is housed in the BMNH collections of The Natural History Museum, London, and these have registration numbers prefixed by B, BB, or BD. Register numbers of specimens in the Forschungsinstitut Senckenberg, Frankfurt, Germany, have the prefix SMF.

Order **RHYNCHONELLIDA** Kuhn, 1949
Superfamily **PUGNACOIDEA** Rzhonsnitskaya, 1956
Family **ASEPTIRHYNCHIIDAE** Savage, 1996

DIAGNOSIS. Pugnacoidea lacking dental plates, dorsal median septum or septalium; fold and sulcus developed anteriorly.

DISCUSSION. Savage (1996) introduced the family Aseptirhynchiidae, which included *Aseptirhynchia* Soja, 1988, *Brunnirhynchia* Havlíček, 1979, *Carolirhynchia* Havlíček, 1992; *Chalimia* Baranov, 1978 and *Isopoma* Torley, 1934. Xu Han-kui and Yao Zhao-kui (1984: 561, table 3) described a new family, the Katuniidae, in which they placed *Isopoma* Torley, 1934. Savage (1996), in his major revision of Palaeozoic rhynchonellides, placed *Katunia* with weak dental plates in the Leiorhynchinae, while *Isopoma* was assigned to the new family, the Aseptirhynchiidae, which lacks both dental plates and a dorsal median septum. Genera in the family are united by their similar external morphologies, i.e. their posterior smooth shells, and a tendency towards the anterior development of a fold and sulcus in which a few ribs developed. In some, weak additional ribs occur flanking the sulcus. The genera are differentiated principally on their internal characters. In two, *Chilimia* and *Aseptirhynchia*, dental plates are either weakly present or developed only in early ontogeny. Shell wall thickening is variable: in *Chilimia* the walls appear to be thin (Baranov, 1978: text–fig. 1); in *Aseptirhynchia* the ventral valve walls became thickened and overgrew the juvenile dental plates, but the dorsal valve remains relatively thin; in *Isopoma* both valves became thickened, but the hinge plates remain free, and the teeth and sockets are particularly strongly developed; in *Carolirhynchia* and *Brunnirhynchia* the valve wall thickening fused the hinge plates to the dorsal interior, leaving only a groove between the median edges. A further distinction in *Chilimia* is that the hinge plates only became medially disjunct at their anterior extremities.

DISTRIBUTION. *Aseptirhynchia* occurs in the Emsian of Alaska. *Carolirhynchia* was reported originally from Pragian and Emsian beds in the Barrandian area of Bohemia, although Savage (1996) reported the genus as restricted to the Eifelian. *Chilimia* is reported from the Middle Devonian of northeast Russia. *Isopoma* was originally described from the Middle Devonian of Germany, but is fully described below. *Brunnirhynchia* is of Early Famennian age from the Bruno area of the Czech Republic.

Genus *ISOPOMA* Torley, 1934

TYPE SPECIES. *Terebratula brachyptycta* Schnur 1853, by original designation.

DIAGNOSIS. Aseptirhynchid lacking adult dental plates, with dorsal valve thickening confined umbonally and free, disjunct hinge plates extending from well-developed inner socket ridges. Ventral valve thick-walled with prominent teeth. There are no median septa in either valve.

COMMENT. Below we describe or comment on the twelve species described as belonging to *Isopoma*, including one new species. The name *I. brachyptyctum* has been used in Germany to include specimens resembling the lectotype of Schmidt (1941), which are longer than wide, as well as more equidimensional specimens commonly found in the Middle and Upper Givetian strata, typically to the east of the river Rhine, Germany. We provide here some sections taken from both forms but have insufficient information to be able to differentiate these forms clearly, other than by their exteriors. Other species, eg. *I. orthoglossa* (Torley) and *I. ovale* Xian & Jian, somewhat resemble the wide forms of *I. brachyptyctum* and are of similar age. Further studies of these faunas are required to resolve these taxonomical problems and the stratigraphical range of true *I. brachyptyctum*.

SHELL STRUCTURE. The shell structure of *Isopoma* (Figs 19–21) is poorly known; no primary layer has been seen in fresh condition, but the secondary fibres are relatively large and angular; being somewhat rhomboidal in section. This is characteristic of many Palaeozoic rhynchonellids.

Isopoma brachyptyctum (Schnur, 1853) Figs 1–5, 19

1853 *Terebratula brachyptycta* Schnur: 178: pl. 23, fig. 6.

1934 *Isopoma brachyptyctum* (Schnur); Torley: 81, pl. 3, figs 12–15.



Figs 1, 2 *Isopoma brachyptyctum* (Schnur). **1**, syntype; copy of Schnur, 1853: pl. 23, fig. 6; presumed from Eifelian limestone, Blankenheim, Germany; Schnur Collection, Geol.-Paläontological Institute, Bonn; $\times 2$. **2**, lectotype; a syntype from the Schnur Collection resembling that of Fig. 1; copy of Schmidt 1941: pl. 4, fig. 88; locality unspecified, but possibly Ahrdorf Formation, Eifelian, Germany; $\times 2$. Both specimens are illustrated in dorsal, anterior and ventral views, but note that Schmidt illustrated the anterior view with the ventral valve uppermost.

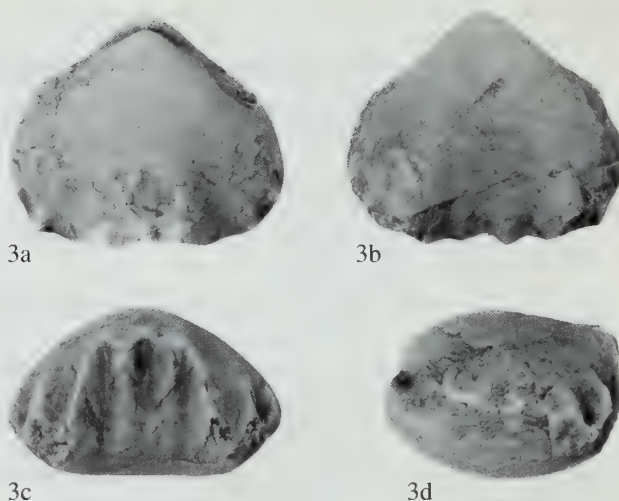


Fig. 3 *Isopoma brachyptyctum* (Schnur). Dorsal, ventral, anterior and lateral views; Givetian Massenkalk, Bilveringsen, Germany; BD 12784, $\times 3$.

1941 *Isopoma brachyptyctum* (Schnur); Schmidt: 45, pl. 4, fig. 88.

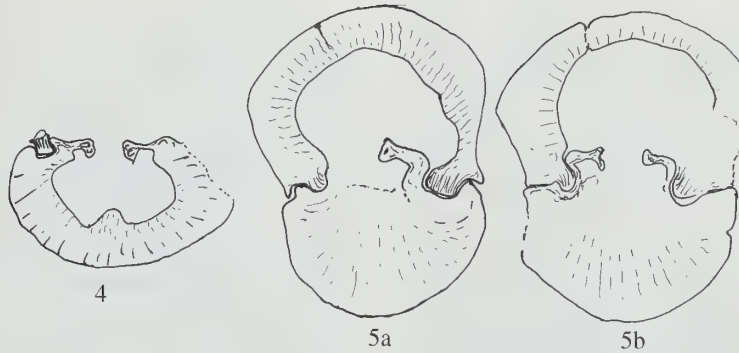
1966 *Isopoma brachyptyctum* (Schnur); Biernat: 106, pl. 22, figs 1–9.

TYPE SPECIMEN. The lectotype, selected by Schmidt (1941: 45, pl. 4, fig. 88), is from Im Kalk zu Blankenheim (Schnur, 1853: 178). Schmidt did not specify the precise stratigraphical level of this specimen, which is in the Schnur Collection at the Geol.-Paläontological Institute, Bonn, Germany. However, the lectotype possibly came from the Ahrdorf Formation (Mohanti, 1972: 170), which is considered to be Middle Eifelian in age (see Paulus, Struve & Wolfart, 1963: 466, text-fig. 1).

DIAGNOSIS. Outline approximately equidimensional, with greatest width at about two-thirds of the length of the shell; ventral sulcation prominent, commonly containing two ribs and an additional pair of ribs lateral to the sulcus; fold weakly developed.

MATERIAL. German specimens from the Eifel region are: 3 specimens (SMF XVII 342b, XVII 342c and XVII Bi) from Bilveringsen; one specimen (SMF XVII 1168a) from Schleddenhof; one specimen (SMF XVII 342k) from the Ahrdorf Formation at Gees; and 5 specimens (SMF XVII 2420) from the Ahabach Formation at Hallert. In addition, unregistered specimens were kindly donated by the late Dr Struve from the upper part of the Lahr Member of the Ahabach Formation (Loc. St. 949) (BD12782–83) and from the Massenkalk (Kohlenstein Member) of the Kohlenstein quarry at Iserlohn-Bilveringsen (BD 12784).

STRATIGRAPHICAL RANGE. According to Schmidt (1941: 45), in the Eifel area of Germany *Isopoma brachyptyctum* ranges from Middle Eifelian (Ahrdorf Formation) to the Fleringen Schichten, which is now known to range from the Ahabach Formation (uppermost Eifelian) to the Curten Formation (Lower Givetian) (Paulus, Struve & Wolfart, 1963: 466, text-fig. 1). The species is also known to the east of the Rhine river in Germany. Torley (1934) described *Isopoma brachyptyctum* (Schnur) from the Massenkalk (Upper Givetian) of Bilveringsen, near Iserlohn. Schmidt (1951) also briefly remarked upon a specimen of *Isopoma brachyptyctum* from the Upper Givetian Flinz kalk of Schleddenhof, near Iserlohn-Letmathe on the east side of the Rhine.



Figs 4, 5 *Isopoma brachyptyctum* (Schnur). **4**, section of a dorsal valve at the socket showing well defined, separated, outer hinge plates and crural bases; Ahbach Formation, Lahr Member, mid-Eifelian, Im Lahr, NE of Niederehe, St. 949, Germany; BD 12782, $\times 9$. **5a, b**, sections through a shell near the socket, where the valve is thickened, slightly posterior and dorsal to that of Fig. 4; Massenkalk, Kohlenstein Member, Upper Givetian, Iserlohn-Bilveringsen, Germany; BD 12783, $\times 9$.

Maillieux (1941: 10) listed *Isopoma aptyctum* (Schnur) and *I. brachyptyctum* from Frasnien (F₂ beds) in the Devonian of Ardenne, Belgium, but gave no description or illustrations, so the validity of these occurrences cannot be verified.

Havlíček (1951, 1961) reported *I. brachyptyctum* (Schnur) from the Middle Devonian (Givetian) limestones in the vicinity of Čelechovice (Moravia). Biernat (1966) described specimens of *I. brachyptyctum* (Schnur) from the Skaly Beds and one from the Pokrzywianka beds, Holy Cross Mountains, Poland. Although there is some difficulty about the Eifelian/Givetian age for the Skaly Beds, Biernat (1966) thought them to be Lower Givetian on the basis of her brachiopod study.

Bulbichenko (1974: 72, 73, pl. 10, figs 8–10) described and illustrated *I. brachyptyctum* (Schnur) from the Krjukovo Beds (Lower? Emsian) of the Russian Rudnogo Altai region. However, serial sections and precise information about the interior is lacking, so the identification is doubtful.

Sapel'nikov & Mizens (1984: 23–24, pl. 4, figs 10, 13, pl. 5, figs 4, 5) described and figured *I. aff. brachyptyctum* (Schnur) from beds with *Ivdelinia acutolobata* of Lower Givetian age from the central part of the Ufa Amphitheatre in the southwest Urals, Russia. Mamedov (1985) reported the occurrence of *Isopoma brachyptycta* in a key section of the Middle Devonian of Transcaucasia, in the upper Arpachaisk sub-suite of Givetian age. He claimed that this interval corresponds with the Alchedatskii horizon of the Kuznetsk Basin, the upper parts of the Starooskolskii (old Oskolskii) horizon (Mulinskii/Moulins beds) on the Russian platform and possibly the upper parts of the Aidarlinskii horizon of Kazakhstan. According to Mamedov (1985: 159) the Mont-Aur Layers with *Hexagonaria quadrigemina* in the Ardennes correspond to this interval and the Boldsdorf layers in the Eifel are possibly synchronous.

Sapel'nikov & Mizens (1985), while providing new data on the biostratigraphy of the Ural Mountains, recorded *Isopoma aff. brachyptyctum* on both western and eastern slopes, at a stratigraphic level which they correlated with the Eifelian-Givetian horizons of the Ardennes-Rhine region of Western Europe.

Xian Si-yan & Jiang Zong-long (1978: 289, pl. 106, fig. 14) described and illustrated *I. brachyptyctum* (Schnur) from the lower part of the Dushan Formation (Givetian), Dongyao, Xiasi, Dushan County, Guizhou, China. Although no internal information was given, the shape resembles that of the lectotype figured by Schmidt (1941: 45, pl. 4, fig. 88). Xian & Jiang (1978) did not give detailed

information on the stratigraphic levels from which their two species (*I. brachyptyctum* and *I. ovale*) were found.

Isopoma alecto (Barrande, 1847)

1847 *Terebratula alecto* Barrande: 42, pl. 20, fig. 2.

1961 *Isopoma alecto* (Barrande); Havlíček: 40, pl. 6, fig. 5.

COMMENT. This species was described from the Pragian of Bohemia. Havlíček's (1961) redescription showed that it is characterized by a ventral sulcus starting just before half the valve length and containing three ribs. Havlíček (1961: 40, text-fig. 7) also gave a section showing a thin divided hinge plate and crural bases, which are directed dorsally, as in all known *Isopoma* species. Havlíček (1992: 56, table 1) listed this species in the Suchomasty Limestones (Dalejan). The species name was used by Perry (1984) for specimens from the Upper Lochkovian of the Yukon Territory in Arctic Canada. However, we think more critical studies are necessary before accepting the Yukon forms as true *Isopoma*.

Isopoma gryps Schmidt, 1965

Fig. 6

1965 *Isopoma gryps* Schmidt: 13–16, text-figs 18, 19; pl. 1, figs 1–7.

MATERIAL. From Greifenstein, Eifel region, Germany, 17 specimens (SMF 19531) and two unregistered specimens, donated by the late Dr Struve, from an exploration trench from the Greifensteinkalk of the same area (BD 12786–87).

COMMENT. This species was originally described from the Lower Eifelian Greifensteiner Kalk of the Eifel region. It is characterized by a prominent ventral sulcus, which originates close to the umbo. In some specimens the sulcus contains a single median rib. Serial sections (Fig. 6a–c) show characters typical of the genus, with a thickened dorsal umbo and prominent teeth.

Isopoma hertae Mohanti, 1972

Figs 7, 8

1972 *Isopoma hertae* Mohanti: 170, pl. 6, fig. 4, pl. 7, figs 1–5.

COMMENT. Specimens were originally described from the upper Eifelian to Givetian transitional beds in the Cantabrian Mountains, northern Spain, and these have been studied. This species is characterized by a circular to subpentagonal outline, weakly developed

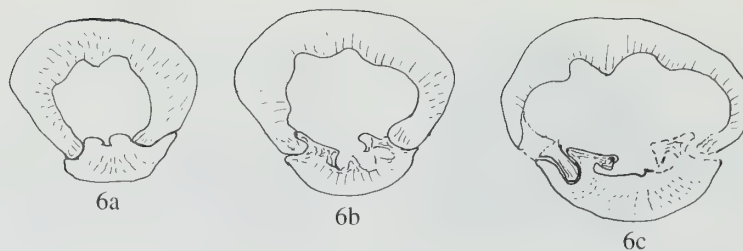


Fig. 6 *Isopoma gryps* Schmidt. Sections through the socket region of a poorly preserved specimen showing thickened valves. Greifenstein Kalk, Lower Eifelian, trench at Wiege, Greifenstein, Hessen, Germany; BD 12786, $\times 9$.

uniplication modified by a zig-zag commissure resulting from 6–7 short, anteriorly confined ribs. The ventral valve is further ornamented by a median groove originating close to the umbo.

Isopoma hertae has also been recorded by Ficner & Havlíček (1978) from the Lower Givetian beds of the Čelechovice area in Moravia, Czech Republic.

Isopoma isiliense Rzhonsnitskaya, 1953

1953 *Isopoma isiliensis* Rzhonsnitskaya: 177, pl. 10, figs 12, 13.

COMMENT. The only known occurrence is the original description of specimens from the Upper Frasnian of the Kuznetsk Basin,



Fig. 7 *Isopoma hertae* Mohanti. Dorsal, ventral, anterior and lateral (anterior uppermost) views; Portilla Formation (Eifelian to Givetian) of southern Cantabrica, Spain; BD12734, $\times 3$.

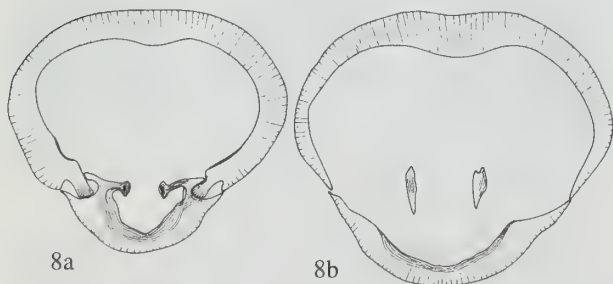
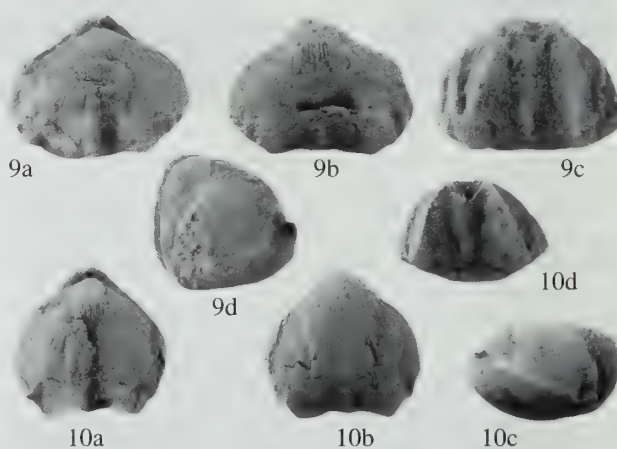


Fig. 8 *Isopoma hertae* Mohanti. Portilla Formation (Eifelian to Givetian), Cantabrica, Spain; sections of the specimen figured by Mohanti (1972: figs 30.2, 30.3); specimen not registered, Geologisch en Mineralogisch Instituut, Rijksuniversiteit, Leiden, $\times 8$.



Figs 9, 10 *Isopoma lummatoniensis* (Davidson). **9a–d**, *Lectotype*, here selected (figured Davidson, 1865: pl. 14, fig. 14); dorsal, ventral, anterior and lateral views with the umbo to the right; late Givetian, Lummaton, Devon; BB 61841, $\times 3$. **10a–d**, dorsal, ventral, anterior and lateral views (with the umbo to the left); late Givetian, Lummaton, Devon; B 12802, $\times 3$.

Russia (Rzhonsnitskaya, 1953). The species is poorly characterized, but appears to be rather small and deep bodied, with 3 ribs in the ventral sulcus. Interiors are unknown.

Isopoma lummatoniensis (Davidson, 1865) Figs 9–11, 21

1865 *Rhynchonella lummatoniensis* Davidson: 70, pl. 14, figs 14–17.

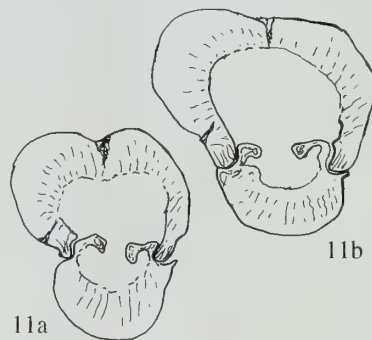


Fig. 11 *Isopoma lummatoniensis* (Davidson). Sections through the socket and hinge plate region. Lummaton Shell Bed, late Givetian, Lummaton, Devon; BB 51959, $\times 9$.

?1953 *Isopoma lummatoniensis* (Davidson); Rzhonsnitskya: 176, pl. 10, figs 14, 15.

TYPE SPECIMEN. BB 6184, figured by Davidson (1865: pl. 14, fig. 14), is here selected lectotype (Fig. 9a–d).

COMMENT. Davidson (1865), described a series of quarries at Lummaton, about 3 miles north of Torquay, Devon. He referred to the beds as the Stringocephalus Burtini Beds. The Lummaton Shell Bed is part of this series of late Givetian fossiliferous limestones. Davidson (1882: 11) said Rigaux (1878) had recorded *Rhynchonella lummatoniensis* at Ferques, France. However, the extensive ecological study by Wallace (1966; 1969) in that area did not record the species, so we are doubtful about *Isopoma* occurring at Ferques.

The species is characterized by its high ventral sulcus containing a single rib and the deep body cavity; the dorsal valve has a corresponding long narrow median groove. Davidson (1865: pl. 14, fig. 15) figured a second syntype of *Rhynchonella lummatoniensis* which is less deep-bodied and has two ribs in the ventral sulcus. This might be conspecific with the lectotype, but it recalls the similarly shallow specimen of *I. maymyoensis* described below. Large collections might reveal whether these shallower specimens with more ribs are really conspecific.

Rzhonsnitskya (1953: 176, pl. 10, figs 14, 15) recorded and illustrated *I. lummatoniensis* from the Frasnian of the Kuznetsk Basin, Russia, but internal structures of these specimens are very poorly known and generic assignment remains in doubt.

Isopoma maymyoensis sp. nov.

Figs 12–14, 20

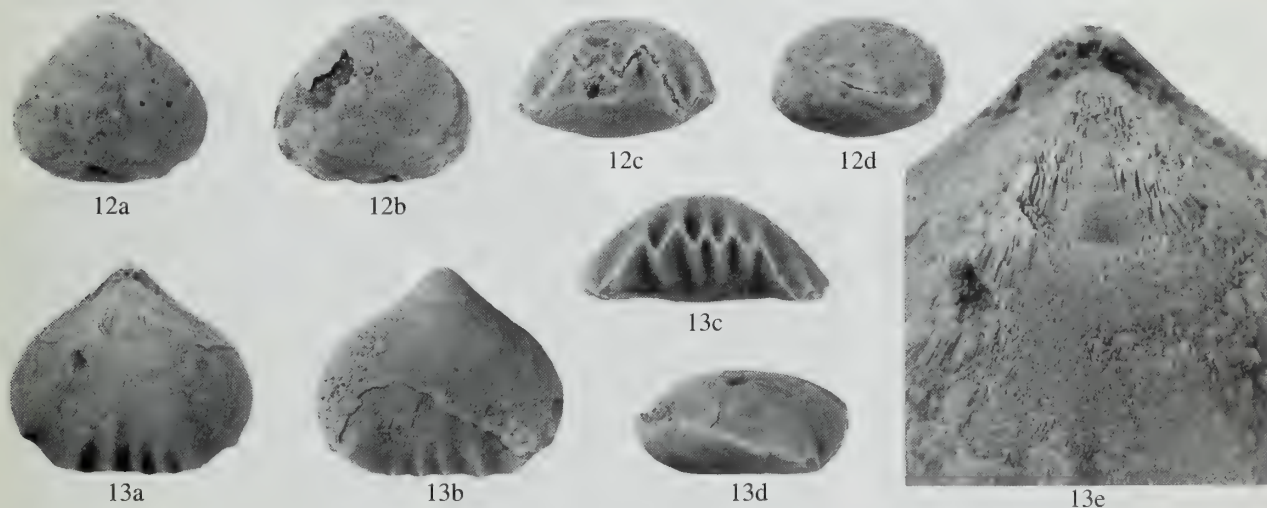
1969 *Uncinulus subsignata* Reed; Anderson *et al.*: 137, pl. 5, figs 18–21 (*non* figs 22–31).

ETYMOLOGY. The species is named from Maymyo, Burma, the region from which the material was collected.

TYPE SPECIMEN. The holotype (BB 55546; figured Anderson, Boucot & Johnson, 1969: pl. 5, figs 18, 19) is from the Padaukpin Limestone (late Eifelian to early Givetian), Padaukpin, 10 miles NE of Maymyo, Central Burma.

DIAGNOSIS. *Isopoma* with relatively shallow body cavity and weakly developed uniplication modified by 1–3 short ribs within the sulcus; an additional pair of ribs may occur laterally; hinge plates well separated both medially and from the dorsal valve floor.

COMMENT. Anderson *et al.*'s (1969) description of *Uncinulus subsignata* included smaller specimens which are here called *Isopoma maymyoensis*, as well as larger specimens (Anderson *et al.*, 1969: pl. 5, figs 22–31) which we accept as *Nalivkinaria subsignata* (see Mohanti, 1972: 166). The age of the *Isopoma* specimens, together with *Nalivkinaria*, was originally given as probably Eifelian, but we extend the age of the beds into the Early Givetian (Mohanti & Brunton, 1992: 11). Ecologically *Isopoma maymyoensis* thrived in a shallow marine subtidal benthic level-bottom environment and the associated carbonates contain a variety of shelly fossils.



Figs 12, 13 *Isopoma maymyoensis* sp. nov., late Eifelian to lower Givetian, Padaukpin Limestone, Padaukpin, Burma. 12a–d, Holotype; dorsal, ventral, anterior and lateral views (note that the umbo is broken); BB 55546, $\times 4$. 13a–d, dorsal, ventral, anterior and lateral views, $\times 4$; 13e, detail of part of the dorsal valve, BB 55547, $\times 10$.



Fig. 14 *Isopoma maymyoensis* sp. nov. Sections at the sockets and hinge plates and anteriorly through the crura. Padaukpin Limestone, Burma, BB 55547, $\times 9$.

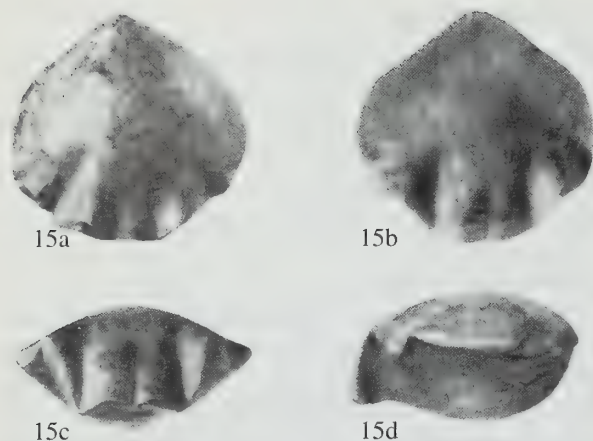


Fig. 15 *Isopoma orthoglossa* (Torley). *Lectotype*; dorsal, ventral, anterior and lateral views (with ventral valve uppermost); Flinzkalk, Givetian, Iserlohn, SMF XVII 1164a, $\times 2.5$ (from Schmidt, 1951: pl. 1, fig. 6).

***Isopoma nekhoroshevi* Bublichenko, 1974**

1974 *Isopoma nekhoroshevi* Bublichenko: 73, text-fig. 9; pl. 2, fig. 9.

COMMENT. This species is from the Emsian of the Rudnogo Altai, Ural Mountains, Russia. The specimens are small, the ventral sulcus starts near the ventral umbo and ribbing is confined anteriorly, associated with the fold and sulcus. The hinge plate appears to be divided (Bublichenko, 1974: text-fig. 9) and the lack of a median septum is normal for the genus.

***Isopoma orthoglossa* (Torley, 1908)**

Fig 15

1908 *Camarophoria orthoglossa* Torley: 29, pl. 3, figs 20, 21, pl. 4, figs 1–3.

1951 *Isopoma orthoglossa* (Torley); Schmidt: 87, pl. 1, figs 6a–d.

COMMENT. Schmidt (1951) redescribed this species from the Flinzkalk (Upper Givetian) in the Iserlohn-Letmathe area on the east side of the river Rhine, Germany. The lectotype (Schmidt, 1951: pl. 1, fig. 6) is comparable to the wide Givetian specimens of *Isopoma brachyptyctum*. No information on internal structures was given by Schmidt. Further work on this species and the wider form of *I. brachyptyctum* from the Upper Givetian of the eastern Rhine area is needed to establish their relationships. We have studied two specimens from Bilveringsen (SMF XVII 478a), but have not been able to prepare sections.

***Isopoma ovale* Xian Si-yan & Jiang Zong-long, 1978**

1978 *Isopoma ovale* Xian & Jiang: 289, pl. 106, fig. 13.

COMMENT. *Isopoma ovale* is from the lower part of the Dushan Formation (Givetian), Dongyao, Xiasi, Dushan County, Guizhou, China. Externally this species somewhat resembles the wider forms of *I. brachyptyctum* found in the Upper Givetian strata of Germany. Xian & Jiang (1978: 289) record 'dental plates fused with the wall of shell'. However, we have seen no evidence of dental plates as compared to simple shell wall thickening. They also report that crural plates and hinge plates are separated and the cardinal process absent. *I. ovale* differs from the type species in being wider in outline, having a weak sulcus and 7 to 8 anterior ribs close to the commissure.

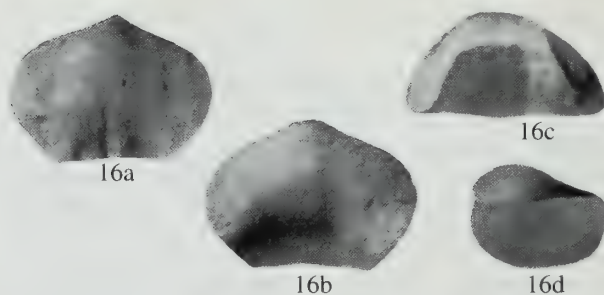


Fig. 16 *Isopoma? ren* Schmidt. *Holotype*, dorsal, ventral, anterior ($\times 2$) and lateral views; Flinzkalk, Schleddenhof bei Iserlohn; SMF XVII 1163a, $\times 1.7$ (from Schmidt, 1951: pl. 1).

***Isopoma? ren* Schmidt, 1951**

Fig. 16

?1908 *Camarophoria aptycta* (Schnur); Torley: 30, pl. 6, figs 4, 5.
1951 *Isopoma? ren* Schmidt: 88, pl. 1, fig. 4.

COMMENT. Schmidt assigned her species doubtfully to *Isopoma*; it is from the Upper Givetian Flinzkalk in the Iserlohn-Letmathe area, Germany. The figured specimen (Schmidt, 1951: pl. 1, fig. 4) appears to be somewhat wider than *I. brachyptyctum*, deeper bodied and has indistinct ribs. Schmidt described a divided hinge plate, weakly curved and ventrally directed crura, and the absence of an internal median septum, all features that are consistent with *Isopoma*. We have seen two specimens from Schleddenhof (SMF XVII 1163b, 1163c), but have not been able to prepare sections for internal study.

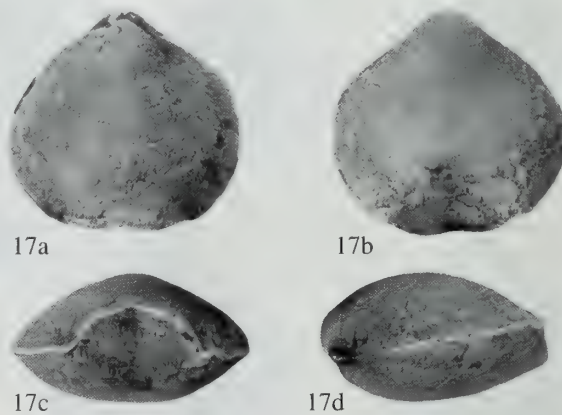


Fig. 17 *Isopoma xestum* Torley. Dorsal, ventral, anterior and lateral views; Givetian, Massenkalk, Bilveringsen, Germany; BD 12785, $\times 3$.

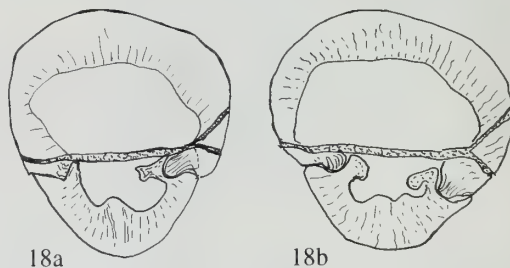


Fig. 18 *Isopoma xestum* Torley. Sections through the specimen from Massenkalk, Germany, figured in Fig. 17, $\times 9$.

Isopoma xestum Torley, 1934

Figs 17, 18

1934 *Isopoma xestum* Torley: 82, pl. 3, figs 16, 17.

COMMENT. This species is from the Upper Givetian Massenkalk of Bilveringsen near Iserlohn on the east of the Rhine, Germany. The figured specimens are small and less deep than typical *I. brachyptyctum* and do not show ribbing. We have studied 11 specimens (SMF XVII 347c) and an unregistered specimen, donated by the late Dr Struve, from the Kohlenstein member of the Massenkalk at the Kohlenstein quarry in the Iserlohn Bilveringsen area (BD 12785). The sectioned specimen was not well preserved so the internal features remain poorly known and reference of the species to *Isopoma* remains insecure.

STRATIGRAPHIC AND GEOGRAPHIC DISTRIBUTION OF *ISOPOMA*

Twelve species of *Isopoma* are described or commented upon above; *I. aptyctum* (Schnur), of supposed Frasnian age, is very poorly known, and we have not been able to study specimens, so we do not describe it here. Of these twelve reasonably established species, eight are from the Eifelian to Givetian of the Middle Devonian, and two (*I. alecto* (Barrande) and *I. nekhoroshevi* Bublichenko) from the Pragian and Emsian of the Lower Devonian are doubtfully referred to *Isopoma*. Two more species (*I.?* *ren* Schmidt and *I. xestum* Torley), from the upper Givetian might belong to *Isopoma*, but they are also poorly known. We, therefore, suggest a well established stratigraphical range for *Isopoma* in the Eifelian and Givetian, with less securely established species in later Lower Devonian rocks.

Isopoma appears to be absent from the Devonian of Morocco (Drot, 1964) and Afghanistan (Durkoop, Mensink & Plodowski, 1967; Durkoop, 1970). Brice (1971), however, described specimens from Afghanistan as *Kransia?* cf. *subsignata* (Reed, 1908), and

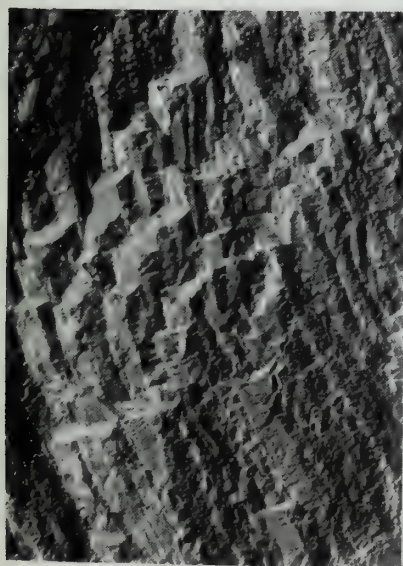
suggested they are conspecific with specimens from Burma figured by Anderson, Boucot & Johnson (1969) as *Uncinulus subsignata* (Reed). We do not think Brice's (1971) illustrations belong to what would now be called *Nalivkinaria subsignata*, or to either *Beckmannia* or *Isopoma*.

The palaeogeographical map (Fig. 22) shows the distributions of *Isopoma* species.

PALAEOBIOGEOGRAPHY

Devonian brachiopod biogeography has been discussed in detail by Boucot (1988). *Isopoma* is typically a Middle Devonian brachiopod belonging to the Rhenish-Bohemian Region of the Old World Realm (Boucot, 1984) and has Rhenish provincial affinities (Struve, 1982a). The largely warm, shallow marine environment of this biogeographic region probably had complex current circulation patterns. Apart from palaeogeography, sea-level changes and the development of reefs and banks, the shallow seas and patterns of marine circulation might have influenced the variable faunal associations of the Middle Devonian of the Rhenish-Bohemian Region. Information on the Rhenish-Bohemian Region brachiopods shows them as occurring in parts of Europe, North Africa and Asia. The Lower and Middle Devonian faunas of most of north Africa are of Rhenish-Bohemian Region type (Boucot *et al.*, 1983). The Jauf Formation of Lower Devonian (Pragian-Emsian) age of northwestern Saudi Arabia contains brachiopods and trilobites which also belong to the Rhenish-Bohemian Region of the Old World Realm (Boucot, 1984; Boucot *et al.*, 1989).

A Rhenish type of Eifelian brachiopod fauna occurs in Armenia and the Tien Shan (Boucot *et al.*, 1988: 365). The biostratigraphy and biogeography of Devonian brachiopods in China have been described by Hou Hong-Fei (1981) and Wang Yu *et al.* (1984). The South China Province includes the south Tien Shan Mountains,



19



20



21

Figs 19–21 Scanning electron micrographs of abraded valve exteriors illustrating macro-shell structures in three species of *Isopoma*. **19**, *I. brachyptyctum* (Schnur), Eifel, Germany; same specimen as Fig. 3; ventral valve anterolateral flank, BD 12784, $\times 100$; **20**, *I. maymyoensis* sp. nov., Burma; ventral valve (see Fig. 13), posterior to median sulcus, BB 55547, $\times 50$; **21**, *I. lummatoniensis* (Davidson); Devon, England; ventral valve, posterolateral flank, BB12802, $\times 40$.

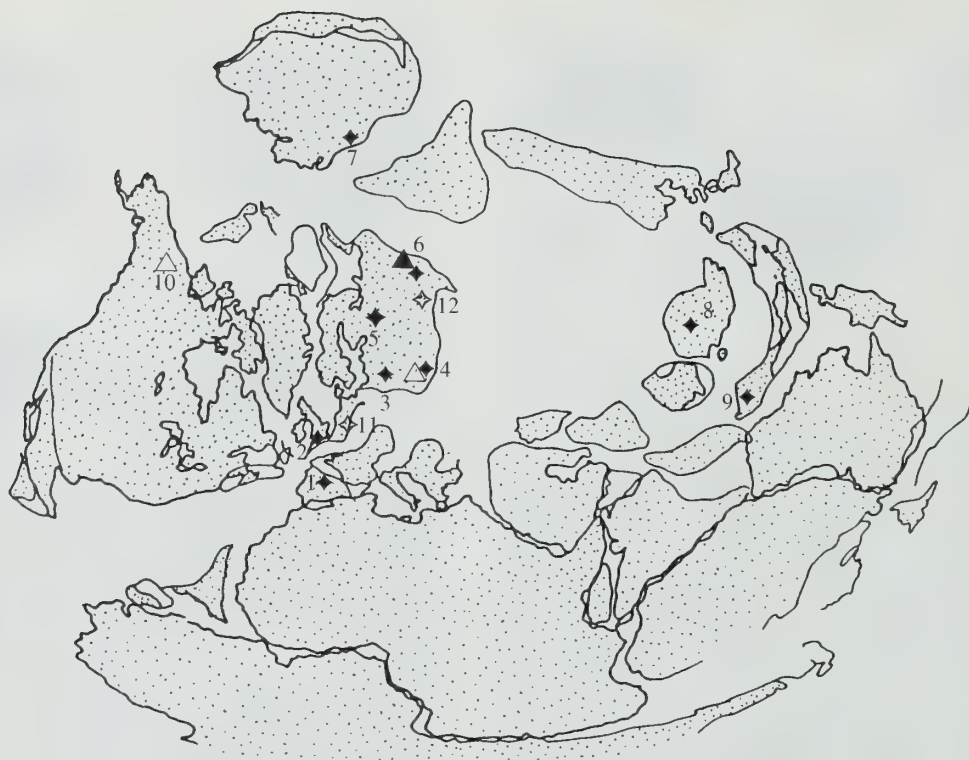


Fig. 22 World palaeogeographical map of the Middle Devonian (from Scotese & McKerrow, 1990) showing the distribution of *Isopoma* species. Δ – Lower Devonian, Pragian; \blacktriangle – Lower Devonian, Emsian; \blacklozenge – Middle Devonian, Eifelian to Givetian; \diamond – Upper Devonian, Frasnian. 1 – north Spain (*I. hertae*); 2 – Devon, England (*I. lummatoniensis*); 3 – Eifel, Germany (*I. brachyptyctum*, *gryps*, *orthoglossa*, *ren*, *xestum*); 4 – Czech Republic (*I. brachyptyctum*, *hertae*, and in Pragian, *I. alecto*); 5 – Poland (*I. brachyptyctum*); 6 – west Urals (*I. brachyptyctum* and in Emsian, *I. nekhoroshevi*); 7 – east Urals (*I. brachyptyctum*); 8 – Guizhou, China (*I. brachyptyctum*, *ovale*); 9 – Burma (*I. maymyoensis*); 10 – Yukon (*I. alecto*); 11 – Ardennes (*I. aptyctum*); 12 – Kuznetsk, Russia (*I. isiliensis*, ?*I. lummatoniensis*).

which are on the eastward extension of the Ural-Tien Shan marine belt, and brachiopods here are similar to those in Europe, including the Urals. During the early part of the Middle Devonian, three facies-related assemblages of brachiopods existed, reflecting different palaeoecological conditions. *Isopoma* is associated with the *Zdimir* community (Hou Hong-Fei, 1981) and restricted to limestone facies bordering platform areas. The facies is characterized by reefal limestones and biostromes composed of corals and stromatoporoids, together with abundant accumulations of *Zdimir* shells and occasional occurrences of other brachiopod genera. Farther to the north, in western Nei Monggol (Inner Mongolia), Eifelian brachiopods of the Rhenish-Bohemian Region, as well as taxa with Uralian affinities, have been described by Zhang Yan (1985; 1986). This indicates a biogeographic boundary transition comparable to that observed by Nalivikin (in Boucot *et al.*, 1988: 365) from the western Tien Shan. *Camaroforia lummatoniensis*, as recorded by Anderson *et al.* (1969: 118) from the Eifelian of western Yunnan, may belong to *Isopoma*. Adjacent to western Yunnan, Eifelian brachiopods with Rhenish affinities have also been described from the northern Shan State of Burma (Anderson *et al.*, 1969). These Middle Devonian (Eifelian to Lower Givetian) shelly faunas of Padaukpin are strikingly similar to those of the Eifel region of Germany and were first described from Burma by Reed (1908). The brachiopod fauna from the Padaukpin beds can be compared to the Middle Devonian Rhenish brachiopod faunas of the European Eifel region, Germany, the southern Cantabrian

Mountains, Spain, and the Holy Cross Mountains, Poland. The presence of *Beckmannia* and *Isopoma* in the Padaukpin brachiopod assemblage adds further evidence for the European Rhenish affinities of this brachiopod fauna as an eastern extension of the Rhenish-Bohemian Region of the Old World Realm. In view of the global high level of provincialism during the Eifelian, the similarity of the Middle Devonian shelly faunas of Padaukpin, Burma, to those of the distant Eifel region in Germany seems to be a biogeographic anomaly (Boucot *et al.*, 1988), as was also emphasized by Struve (1982b).

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